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STUDIES IN THE GENUS *COCCOLOBA*, VII.  
A SYNOPSIS AND KEY TO THE SPECIES IN MEXICO  
AND CENTRAL AMERICA \*

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*Coccoloba macrophylla* Sessé & Mociño, Fl. Mex. ed. 2. 96. 1894.

Although *Coccoloba macrophylla* appears to be published as a new epithet in the "Flora Mexicana," the name is a later homonym of *C. macrophylla* Desf. ex Hook. (see Jour. Arnold Arb. 38: 225-227. 1957), a synonym of *C. rugosa* Desf. There are no specimens cited by number in the work of Sessé and Mociño and all of their collections I have seen which bear the name are to be referred to *C. rugosa*. *Coccoloba rugosa* is endemic to Puerto Rico and the species is attributed to Mexico in error.

*Coccoloba manzanillensis* Beurling, Prim. Fl. Portobello in Kongl. Vetensk. Akad. Handl. 142. 1854; Lindau, Bot. Jahrb. 13: 209. 1890.

*Campderia nematostachya* Grisebach, Bonplandia 6: 4. 1858.

*Coccoloba nematostachya* Lindau, Bot. Jahrb. 13: 208. 1890.

The original description of *Coccoloba manzanillensis* cited *Billberg 234* as the type collection and Lindau reported seeing specimens from the Berlin herbarium and from Stockholm. The fragment at Berlin which Lindau annotated is *Billberg 230*, although the Stockholm specimen, presumably the origin of the fragment, is correctly numbered *Billberg 234*. The collection was made on the island of Manzanilla near the port which Lindau called Puerto Belo, known on modern maps as Porto Bello.

The name of this species was originally spelled "manzinellensis" by Beurling, but the spelling was changed to "manzanillensis" by Lindau. While the island where Billberg collected the type specimen is not on modern maps, Beurling's intention in describing the species is obvious. "Manzanillo," or "little apple" in Spanish, is commonly applied to the widespread and infamous strand plant *Hippomane manchineel* and although Lindau failed to comment on his correction of an orthographic error or to cite the original spelling, it seems desirable to allow this correction to stand.

\* Continued from vol. XL, p. 203.

*Campderia nematostachya* Griseb., transferred to *Coccoloba* by Lindau, is based on an unnumbered Andersson specimen from Panama. A specimen from the Meisner herbarium, now at the New York Botanical Garden, appears to be identical with the Göttingen specimen and part of the Andersson collection. A label bears Grisebach's handwriting, but unfortunately it carries the legend, "*Coccoloba jagifolia* Guadeloupe? coll. Duchassaing." The label is obviously incorrect.

Lindau recognized both *Coccoloba nematostachya* and *C. manzanillensis*. He distinguished them by placing *C. manzanillensis* in a group of species having glabrous leaves, while associating *C. nematostachya* with species having persistent pubescence. However, examination of the specimens cited shows the distinction which Lindau established to be untenable, since it is based on the age of the specimen. *Coccoloba nematostachya*, therefore, must be considered to be the same as *C. manzanillensis*. A long foliar ocrea distinguishes this species which is further characterized by having long, almost silky, hairs.

The Shattuck specimen cited carries a plant of *Oryctanthus cordifolius* as a parasite.

*Bailey 42* is the first mature specimen with fruit.

Panamá. CANAL ZONE: Barro Colorado Island, L.H. & E.Z. Bailey 42 (F), Shattuck 425 (F); between Gatún and Lion Hill, Pittier 2570 (NY). COLÓN: Porto Bello, Billberg 230 (B). DARIÉN: La Palma, Pittier 6599 (GH). PANAMÁ: Pacora, Allen 3450 (A, BRUX, F, MO). Province unspecified: location unspecified, Andersson s.n. (GOET-type of *C. nematostachya*; B, NY), Billberg 234 (F-photo; s).

***Coccoloba matudai* Lundell, Contr. Univ. Mich. Herb. 7: 8. 1942.**

Further study of populations in the field may prove this species to be a hybrid, possibly of *Coccoloba belizensis* and *C. montana*. However, the collections assigned here show an even greater range of leaf size, shape and texture than is normally found in either species. Lundell described both staminate and pistillate flowers, the former apparently from *Matuda 2002* and the latter from *Matuda 4315*. No fruits were formed. The species at present is recognizable only through the character of the branched inflorescence.

México. CHIAPAS: Finca Olvido, Mapastepec, *Matuda 2002* (A, MICH, NY, US); Saxchanal, Sierra Madre, *Matuda 4315* (MICH-holotype; A); Cascada, Siltepec, *Matuda 5144* (F, GH).

***Coccoloba montana* Standley, Jour. Wash. Acad. 13: 368. 1923.**

*Coccoloba escuintlensis* Lundell, Phytologia 1: 213. 1937.

*Coccoloba schippii* Lundell, Bull. Torrey Club. 66: 594. 1939.

*Coccoloba steyermarkii* Standley, Publ. Field Mus. Bot. 22: 138. 1940.

It is unfortunate that the oldest name to be applied to this taxon is based on a sterile, fast-growing shoot. In describing *Coccoloba montana* Standley suggested that the "leaves of this *Coccoloba* are so distinct from



those of other Central American species that it seems desirable to give it a name for purposes of reference."

In the Flora of Guatemala (Fieldiana Bot. 24: 115. 1946) Standley and Steyermark suggested that the material represented is from "*C. escuintlensis* or perhaps of one of the other species listed." The specimens cited below include sterile shoots, as well as fertile specimens, but unfortunately no collections of both sterile, fast-growing shoots and fertile branches have been made from a single plant. Nevertheless, it appears certain that only one species is represented here. A pubescence in the axils of the veins and along the midrib appears in some of the specimens cited, but the leaves are usually glabrous when mature.

*Coccoloba schippii* was described by Lundell and the suggested relationship was with *C. guyanensis* Meisner. This was apparently made on the basis of the sessile flowers which were in bud, appearing in a "spicate" inflorescence. In their key to the Guatemalan species, Standley and Steyermark distinguished *C. schippii* on the characters of sessile flowers, conspicuous nerves and short racemes, but the type of *C. schippii* is obviously a branch with an immature inflorescence. Comparable inflorescence branches can be found on many of the other specimens cited. I believe the mature inflorescence of *C. schippii* as defined by Lundell would be elongated and the flowers would be borne on longer pedicels. *Coccoloba schippii*, with *C. escuintlensis*, seems properly referred to the synonymy of *C. montana*.

In describing *Coccoloba steyermarkii* Standley noted "the species is remarkable for its narrow leaves, more elongate and narrower than those of any other Central American species except *C. acuminata* HBK., to which it is not closely related. It is similar to *C. escuintlensis* Lundell [*C. montana*], of the Pacific slope of Guatemala and of Chiapas, but that has broader leaves, almost concolorous and with much fewer nerves." I have examined sufficient material of *C. montana* to be certain that the type specimen of *C. steyermarkii* can safely be included in *C. montana*. The few specimens which have been assigned to *C. steyermarkii* differ at most in a slightly more coriaceous texture to the leaves and less venation. In all other characteristics I have been able to compare, these same specimens agree well with material here considered as *C. montana*.

*Coccoloba montana* appears to be similar to *C. padiformis* which was described from South America and is represented by recent collections from Panama and Costa Rica. In all specimens seen the apex of the leaf is acute or acuminate, while *C. padiformis* has a rounded or obtuse leaf apex.

**México.** CHIAPAS: Escuintla, *Matuda* 413 (MICH-holotype of *C. escuintlensis*; A, F, GH); Acacoyagua, *Matuda* 17410 (F); Esperanza, Escuintla, *Matuda* 4143, 4145 (A, F, GH, MICH), 17466, s.n. (F). **British Honduras.** TOLEDO DISTRICT: at the British Honduras-Guatemala boundary, *Schipp* S-687 (F-holotype of *C. schippii*).

**Guatemala.** ESCUINTLA: Río Guacalate, *Standley* 60190, 89302 (F); between Río Jute and Río Pantaléon, *Standley* 63464 (F, MICH), 63488 (F); Las Lajas, *Standley* 64787 (F). IZABAL: Puerto Barrios, *Standley* 25075 (US). QUEZALTE-

NANGO: Colomba, *Skutch* 2022 (A, F); Finca "Pirineos" below Santa María de Jesús, *Standley* 68207 (F); between Finca "Pirineos" and Patzulín, *Standley* 86954 (F), 86964 (MICH); between Santa María de Jesús and Calahuaché, *Steyermark* 33677 (F); Calahuaché, *Steyermark* 35473 (F); Río Dulce, west of Livingston, *Steyermark* 39533 (F-type of *C. steyermarkii*), 39404 (F). RETALHULEU: between Retalhuleu and Nueva Linda, *Standley* 87219 (F, US), 87291, 88516 (F); Ajaxá, east of Santa Cruz Muluá, *Standley* 88220, 88232 (F); vicinity of Retalhuleu, *Standley* 88604, 88807 (F, MICH); between Asintal and Colomba, *Standley* 87876 (F). SAN MARCOS: Río Mopá, below Rodeo, *Standley* 68770 (F); Finca Vergel, near Rodeo, *Standley* 68949, 68952 (F); Finca El Porvenir, *Steyermark* 37601 (F, MICH), 52336 (F). SUCHITEPÉQUEZ: Pueblo Nuevo, *Standley* 66936 (F).

El Salvador. AHUACHAPÁN: Sierra de Apaneca, region of Finca Colima, *Standley* 20061 (US-holotype of *C. montana*; GH). LA LIBERTAD: near Comasagua between Finca Germania and Finca San Antonio, *Carlson* 238 (F).

*Coccoloba nicaraguensis* Standley & L. Williams, *Ceiba* 3: 198. 1952.

This species is based on material which is inadequate for an accurate analysis. All the specimens available to me were collected in the mountains at an altitude of 1050–1350 m. west of Jinotega, Department of Jinotega, Nicaragua. The four numbers cited in the original description are *Standley* 9768, 10194, 10233 and 10409, the last of which is the holotype in the herbarium of the Chicago Natural History Museum. A fifth number, *Standley* 10318, was also referred to this species by the original authors by annotation, but was not cited in their paper. The type, *Standley* 10409, and one other, *Standley* 9768, bear young developing leaves which have turned black on drying. Another collection, *Standley* 10233, bears both mature leaves as well as young blackish leaves comparable to the type. The other sheets are of mature branches. Only the type sheet bears flowers and this specimen has four immature inflorescences. On the basis of the sterile specimens with mature foliage, the material would be referred unhesitatingly to *Coccoloba diversifolia*, for it is strictly comparable to material described by Lundell as *C. lancifolia* and later referred by Standley and Steyermark to *C. laurifolia*, a species which is here called *C. diversifolia*. However, as indicated in the original description, the young inflorescence axis is minutely puberulent when seen under a microscope. In this characteristic the species is similar to *C. cozumelensis*. *Steyermark* 45669, from Cerro Chinajá, Department of Alta Verapaz, Guatemala, referred to *C. diversifolia* (*C. laurifolia* Standley & Steyermark), is an accurate match except for a glabrous inflorescence rachis.

*Coccoloba novogranatensis* Lindau, *Bot. Jahrb.* 13: 192. 1890.

*Coccoloba caribaea* Urban, *Symb. Ant.* 5: 337. 1907.

*Coccoloba waitii* Johnston, *Sargentia* 8: 122. 1949.

The typification of this species has been discussed in an earlier paper where the lectotype was designated as *Triana* 978 (P), Bogotá, Colombia (*Jour. Arnold Arb.* 40: 85–87. 1959). For over sixty years no collections



have been assigned to *Coccoloba novogranatensis*. This is a wide-ranging species found at lower elevations and along the seacoast. The sole exception is *R. S. Williams* 945, a collection of very young material from an altitude of 2800 feet in Panama. Additional material from this area may prove this to be *C. obovata*, for in both species the leaves are attached above the base of the ocrea. In *C. novogranatensis* the leaf blades are broadest above the middle, while those of *C. obovata* are broadest below the middle. Leaves of adventitious shoots are nearly indistinguishable. The species are clearly distinct, however, in the stages with mature flowers or fruit. The Steyermark collection from Guatemala, also sterile, is referred here, again with some question.

Johnston does not make any specific comparison in describing *Coccoloba waittii*, noting only that "it is a well-marked species." Although all the specimens I have seen from Panama are from the Pacific side of the Isthmus, *C. novogranatensis* is to be expected to be on the Atlantic coast, as well.

This species is known from the Lesser Antilles, Trinidad, Venezuela, Colombia and Peru, in addition to the specimens cited below from Guatemala and Panama.

**Guatemala.** PETÉN: Between Cerro Ceibal and Ceibal, *Steyermark* 46178 (F). **Panamá.** HERRERA: Pesé, *Allen* 802 (F, GH, MO, NY). PANAMÁ: Perlas Islands, Pedro Gonzalez, *Allen* 2602 (MO); San José Island, *Erlandson* 377 (GH), 550 (GH, NY), 216 (GH); *Harlow* 41 (GH); *Johnston* 213 (GH, MO), 230 (GH-type of *C. waittii*; MO), 975, 1306 (GH). DARIÉN: Cana, *Williams* 945 (NY, US).

### *Coccoloba obovata* HBK. Nov. Gen. 2: 176. 1817.

*Coccoloba coriacea* Willdenow ex Lindau, Bot. Jahrb. 13: 194. 1890, not Sagra.

*Coccoloba goudotiana* Weddell, Ann. Sci. Nat. Bot. III. 13: 260. 1849.

*Coccoloba riparia* Lundell, Contr. Univ. Mich. Herb. 6: 11. 1951.

*Coccoloba obovata* HBK. was based on a Humboldt specimen collected in flower in June, 1805, at Honda in Colombia. Although the specimen in the Willdenow Herbarium has been considered authentic, I wish to designate a sheet in the herbarium at Paris as the lectotype since the latter sheet is more complete, in better condition and bears a label with more adequate data than does the specimen in Berlin.

The name *Coccoloba coriacea*, attributed to Willdenow by Lindau (not *C. coriacea* Sagra), was not published by Willdenow but occurs on the label of the lectotype as the first two words of a long polynomial written in one line. On the sheet which Lindau saw in the Willdenow herbarium the label is smaller and the name "*Coccoloba coriacea*" appears as one complete line, the two words being underlined. It is unfortunate that Lindau chose to pay any attention to this binomial which has no standing.

Lundell described *Coccoloba riparia* from Panama but did not discuss the species or indicate affinities or differences. *Coccoloba riparia* as represented by the type specimen is clearly the same as *C. obovata*.

The majority of the specimens cited below from Central America had been identified either as *Coccoloba marginata* or *C. leptostachya*. I con-

sider the former species to be the same as *C. nitida* and *C. guianensis* from Trinidad and northeastern South America. The latter species, *C. leptostachya*, is referred to the synonymy of *C. barbadensis*.

*Coccoloba obovata* is known from Costa Rica, Panama and Colombia. The type is *Humboldt s.n.* from Honda, province of Tolima, Colombia. The type of *Coccoloba goudotiana* is *Goudot s.n.* from San Luis in Colombia.

**Costa Rica.** Peninsula Osa near Puerto Jimenez, *Brenes 12218* (F); *Cufodontis 91* (F); San Rafael de San Ramón, *Brenes 22020* (F, NY); Santo Domingo de Golfo Dulce, *Tonduz 7122* (F, GH, US), *9934* (BR, LE, M).

**Panamá.** CANAL ZONE: Barro Colorado Island, *Aviles 998* (F), *Salvoza 984* (A), *Shattuck 1063* (F), *Starry 298* (F); F. L. Island, *Bangham 593* (A, F); Salamanca Hydrographic Station, *Dodge, Steyermark & Allen 16983* (BR, DS, G, K, MO), *16983a* (BR, K, MICH, MO); *Woodson, Allen & Seibert 1572* (A, F, MO); northwestern part of Canal Zone, *Johnston 1519* (MO); between Tumba Vieja & Salamanca, *Steyermark & Allen 16758* (BR, MO). CHIRIQUÍ: Cerro Galera Chorchá, Gualaca, *Allen 5020* (A, MO); San Félix, *Allen 3655* (A, BR, MO); between San Félix and Cerro Flor, *Allen 1917* (F, GH, MO); Progreso, *Cooper & Slater 270* (US); San Bartolomé, *Woodson & Schery 947* (F, MO); between Río Chiriquí and Remedios, *Woodson, Allen & Seibert 1182* (A, F, MO). COCLÉ: El Valle, *Allen 2229* (MICH-holotype of *C. riparia*).

***Coccoloba padiformis* Meisner, DC. Prodr. 14: 166. 1856.**

*Coccoloba roseiflora* Standley & L. Williams in Allen, Preliminary Index to the Trees of the Golfito-Palmar area, 37. 1952; Rain Forests of Golfo Dulce, 177. 1956.

*Coccoloba padiformis* Meisner is very similar to *C. densifrons* Martius and perhaps is not distinct. At the present time the distinguishing characteristics of *C. densifrons* are the larger leaves, broadest above the middle, and the longer inflorescence rachis. Lindau did not include *C. densifrons* in his key; hence it is difficult to determine his basis of separation.

*Coccoloba candolleana* Meisner is likewise similar, if not identical, and further material is needed for study before drawing the final limits of any of these species. Certainly the specimens of "Goudot 4" cited by Lindau in extending the range of *C. candolleana* from Bahia, Brazil, to Colombia are better referred to *C. padiformis*. The type of *C. candolleana*, *Blanchet 1818*, has a nearly orbicular and umbonate leaf blade. If this is true of the species and not just a growth form, *C. candolleana* can be maintained as a distinct species.

*Coccoloba roseiflora*, credited to Standley and L. Williams by Allen in the latter's book, "The Rain Forests of Golfo Dulce" is not validly published, since it lacks a description in Latin. The holotype in the herbarium of the Escuela Agrícola Panamericana at Tegucigalpa cannot be sent on loan, but I have seen duplicates of the two collections cited by Allen and on the basis of these, refer the species to *C. padiformis*. *Allen 5964* consists of branches with young leaves indicating a completely deciduous



plant. Mature foliage of this species is represented by *Allen 5944* and the Tonduz collection from the same area of Costa Rica.

The species is currently known from Costa Rica, Panama, Venezuela and Colombia. The type is *Moritz 377*, collected near Caracas in Venezuela.

**Costa Rica.** PUNTARENAS: Palmar Norte de Osa, *Allen 5944* (F-isotype of *C. roseiflora*), 5964 (F); Santo Domingo de Golfo Dulce, *Tonduz 7119* (A, F, GH), 7120 (A, F, GH).

**Panamá.** CANAL ZONE: South of Fort Sherman, *Johnston 1737*, 1814 (MO); Quebrada Ancha, *Steyermark & Allen 17101* (MICH, MO); Río Indio de Gatun, *Pittier 2785* (GH).

***Coccoloba parimensis*** Benthām in Hooker, Lond. Jour. Bot. 4: 626. 1845.

*Coccoloba parimensis* var. *schomburgkii* Meisner, Fl. Bras. 5(1): 35. 1855.

*Coccoloba excelsa* var. *glabra* Lindau, Bot. Jahrb. 13: 171. 1890.

*Coccoloba bracteolosa* Meisner, Fl. Bras. 5(1): 30. 1855.

*Coccoloba paraensis* Meisner, Fl. Bras., 5(1): 38. 1855.

The habit of this plant has accounted in part for the confusion surrounding its description in botanical literature. With regard to the collections studied here, the specimens have been described as a liana, a slender climber, a small tree, a tree, or a tree with scrambling branches. As for the varying leaf aspects which have been described, many of which are cited below, there is no question in my mind that they can be associated with the growth habits of the plant. Other species in northern South America also show the habit of a woody, tree-like plant with scrambling branches. The branches are often so thin and tenuous as to be liana-like in character. Collections made from older plants or those growing in isolated situations show a tree-like habit. Collections from the ends of branches or from plants growing in thickets are likely to be considered liana-like.

Most of the specimens I have seen are in fruiting condition. One specimen, *Maxon & Harvey 6700* from Panama, is in flower and has been cited by Lundell as *Coccoloba bracteolosa* Meisn. (Contr. Univ. Mich. Herb. 6: 9. 1941). The type specimen of *C. bracteolosa* was a staminate flowering specimen and all specimens I have seen referred to this species have likewise been in flowering condition. The same is true for *C. parimensis*. *Coccoloba paraensis*, however, was based on fruiting material and only fruiting material has been referred to this species since.

The numerous specimens from Barro Colorado island were all collected near the laboratory and are either sterile or in fruit. Nevertheless, the series is elaborate and complete, showing the variation in leaf shape, size and texture between the flowering material called *Coccoloba bracteolosa* and the fruiting material called *C. paraensis*. The thin-textured leaves associated with the flowering condition indicate a tendency towards deciduousness in this species. The mature foliage associated with the fruiting specimens is coriaceous and the leaf blades are umbonate or bullate.

Although this evidence is convincing from the specimens on hand, *Cocco-*

*loba bracteolosa* was based on specimens from Bahia and Alagoas on the east coast of Brazil. It is possible that further collections from that area will show that *C. bracteolosa* is better assigned to the synonymy of *C. ochreolata*. The latter species is distinctive in the shape of the fruit.

*Coccoloba parimensis* was based on a Schomburgk collection, without number, from Rio Parime. Lindau assigned this species to the synonymy of *C. excelsa*. I cannot agree completely with this conclusion and am recognizing these as distinct species to call attention to the problem. Field study and mass collections from one plant are needed. For the present, *C. excelsa* is distinct in being more pubescent on the lower leaf surface and on the inflorescence axis. *Coccoloba excelsa* also appears to have larger hairs which break off and leave clear hair bases or black-colored hair bases, either of which frequently appear as punctations. *Coccoloba parimensis* leaves, in contrast, are only puberulent with minute hairs. When Lindau assigned *C. parimensis* to the synonymy of *C. excelsa* he recognized a glabrous state which he called *C. excelsa* var. *glabra*. Lindau also recognized *C. paraensis* and distinguished between this species and *C. excelsa* on a key character of pubescence being present in *C. excelsa* and absent in *C. paraensis*. Lindau's *C. excelsa* var. *glabra*, therefore, becomes an anomaly in his key.

Meisner divided Bentham's *Coccoloba parimensis*, recognizing two varieties. *Coccoloba parimensis* var. *schomburgkii* contained the type and is assigned here to *C. parimensis*. Meisner's second variety, *C. parimensis* var. *hostmanni*, is better referred to *C. excelsa*.

*Coccoloba paraensis* Meisner was based on an unnumbered Martius specimen from Iquapemirim in the Province of Pará and a Spruce collection, also without number, from Barra in the province of Rio Negro. The latter collection has been distributed with labels written "*Coccoloba* /2/" and printed "In vicinibus Barra, Prov. Rio Negro, coll. R. Spruce, Dec.-Mart. 1850-51." The Spruce specimens appear in many herbaria and all are unidentified. No type was designated by Meisner but the Field Museum has distributed photographs of the Martius collection from the Munich herbarium and indicated this as the lectotype.

I have seen material of this species from Brazil, British Guiana, Colombia, Peru and Panama.

Panamá. CANAL ZONE: Barro Colorado Island, *Aviles* 15 (F), *L.H. & E.Z. Bailey* 219 (F), 654 (GH), *Bangham* 447 (A, F), *Salvoza* 904 (A), *Shattuck* 1123 (F), *Standley* 41099 (A), *Wetmore & Woodworth* 859 (A). PANAMÁ: Juan Díaz region, near Tapia river, *Maxon & Harvey* 6700 (F).

*Coccoloba pubescens* Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

This is a West Indian species which I have seen, studied in the field, collected many times and discussed in a previous paper (Jour. Arnold Arb. 38: 229-231. 1957). Lindau described the species (Bot. Jahrb. 13: 202. 1890), citing, in addition to West Indian collections, a Schiede specimen from "herb. Petrop." credited to Mexico without specific location



and a specimen from "Guyana batava" which Meisner also cited. I have not seen *Kegel 1339* which Meisner cited from Dutch Guiana, nor was it present in the Prodrromus Herbarium at Geneva.

*Coccoloba pubescens* was also credited to the Mexican flora by Standley in his "Trees and Shrubs of Mexico" (page 245), although he uses a later homonym, *C. grandifolia* Jacq., for the species. No recent collections are cited by Standley and none is available to me. This species is conspicuous wherever it occurs and it is difficult to believe that it would be overlooked or not be collected in a flora where sterile material has been the basis of many species.

I have on loan three sheets credited to Schiede from Mexico and identified as *Coccoloba pubescens*. Two of these sheets, one from the Berlin herbarium and one from Paris, were not cited by Lindau and do not bear his annotation label. These sheets bear a number "60" in the same script as the generic name, although the specific name and the collector and locality of "Mexico" are in a different hand and possibly may be different from each other. The sheet from the herbarium at Leningrad bears Lindau's annotation label, as well as a label indicating that the specimen was from Fischer's herbarium and was collected at "la Cuesta grande de Chiconcúraos." There is no indication of the collector (i.e., Schiede), and "Mexico" has been added in a different script.

Schiede's travels in Mexico have been described in Linnaea, volumes four and five, in 1829 and 1830. There are several references to *Coccoloba*. One is referred to as a seacoast plant known as "uva" and this is probably *C. uvifera*. The other two refer to plants collected between Río de Tecoluta and Río de Nantla and at Cambre del Obispo. Neither of these locations fits the data cited above for *Schiede 60*. Lindau refers to three unnumbered Schiede collections, but all are cited by him as having come from "Mexico" without further locality.

All three specimens called "*C. pubescens*" consist of a single leaf and a short piece of branch with a terminal bud. The leaves are large ( $30 \times 28$  cm. and  $38 \times 32$  cm.) and the branch stout (10 mm. diameter), suggesting an adventitious shoot or one of vigorous growth. The leaves are suggestive of *Coccoloba pubescens* and the pubescence distribution and hair type can be matched in recent West Indian collections. However, the terminal bud is not that of the West Indian *C. pubescens* but is that of the Mexican *C. liebmannii* Lindau. Only one collection of *C. liebmannii* (*Ferris 6061* from the vicinity of Manzanillo, Colima, Mexico) is available showing the large leaves of vigorous and adventitious shoots. In the three examples of *Ferris 6061* cited elsewhere in this paper, the specimen consists of a fertile branch in fruit with small leaves (average  $9 \times 3.5$  cm.) and a single detached larger leaf ( $23 \times 13$  cm.). No stem section is available for these larger leaves. The pubescence is similar to that of the Schiede specimens; the terminal bud is the same, though the leaves are smaller.

The Fischer herbarium, particularly in reference to *Coccoloba* specimens, is primarily of fragments from cultivated plants; adventitious shoots and associated leaves are common. It seems likely that the Schiede specimen

cited by Lindau is from a plant cultivated in a greenhouse and that the country of origin given on the label is faulty. However, if the data with the specimen are correct, it is probable that this specimen should be identified as *C. liebmanni* and the record of *C. pubescens* be removed from the Mexican flora. Additional field study of *C. liebmanni* is needed to determine variation in size and shape of the leaves and the terminal buds of vigorous and adventitious shoots.

*Coccoloba reflexiflora* Standley, Publ. Field Mus. Bot. 4: 203. 1929.

*Coccoloba colonensis* Lundell, Contr. Univ. Mich. Herb. 6: 9. 1941.

This species is readily distinguished by the basically obovate-oblong leaves, broadest above the middle, which are borne on pale grayish petioles which, in turn, are borne above the bases of the ocreae. The margin of the leaf is invariably revolute and the upper surface is darker than the lower surface upon drying.

The inflorescence is rarely longer than the leaves and the staminate flowers appear to be reflexed, a character on which Standley based the specific name. However, the fruiting pedicels are at right angles to the inflorescence axis and are 1–1.5 mm. long, exceeding the ocreolae. The fruits are smaller than those of other Central American species and the perianth lobes are imbricate, not coronate, over the obtuse apex of the achene.

*Coccoloba colonensis* was based by Lundell on sterile material. He suggested an affinity with *C. lundellii*, which I have concluded is a hybrid of *C. uvifera* and an unknown parent, possibly *C. reflexiflora*. The type of *C. colonensis* is from an adventitious shoot. In the characteristics of the ocreae and the point of attachment of the petiole, as well as in the color and venation of the leaf blade, the specimen is clearly identical with comparable vegetable adventitious shoots of *C. reflexiflora*.

México. CAMPECHE: Villahermosa, *Lundell 1139* (F, MICH). YUCATÁN: Chichén Itzá, *Steere 1600* (F, MICH). Guatemala. PETÉN: Between Uaxactun & San Clemente, *Bartlett 12815* (F, MICH); Carmelita, *Egler 42-244* (F). British Honduras. BELIZE DISTRICT: Northern River, *Gentle 990* (A, F, LE, MICH); Maskall, *Gentle 1223* (A, F, GH, MICH), *1274* (A, DS, F, GH, MICH), *O'Neill 8557* (A, F, MICH); Sibun Road, southwest of Belize, *O'Neill 8570* (Mich). COROCAL DISTRICT: San Antonio, *Schipp S-614* (F, GH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 488* (A, F), *Meyer 45* (F); Hillbank, *Winzerling I-17* (Y). STANN CREEK DISTRICT: Silk Grass Creek Reserve, *Gentle 2959* (A, MICH). TOLEDO DISTRICT: Monkey River, *Gentle 4150* (A, MICH). District unspecified: Tower Hill, *Karling 15* (F-holotype; US); Manatee Lagoon, *Peck 92* (GH). Honduras. COLÓN: Guarunta, Wisperini Camp, *C. & W. von Hagen* (NY-isotype of *C. colonensis*).

*Coccoloba spicata* Lundell, Bull. Torrey Club 66: 594. 1939.

"*Coccoloba coronata* Jacquin?," Millspaugh, Publ. Field Mus. Bot. 1: 294. 1896.

Lundell compares this species with *Coccoloba mayana* Lundell which I have placed in synonymy with *C. barbadensis* Jacq. The specimens cited



below, with one exception, are those also cited by Lundell in the original publication.

*Coccoloba spicata* was based on staminate flowering material. Only one fruiting collection is known. The species appears distinct in the sessile flowers and densely flowered inflorescence. In fruit the pedicels are scarcely developed and, if present, are less than one-fourth the length of the ocreolae. In contrast to *C. barbadensis*, the apex of the fruit is obtuse to rounded and not at all coronate. The perianth lobes are orbicular and represent the upper third of the fruiting perianth. In sterile condition it is almost impossible to distinguish *C. spicata* from *C. barbadensis*.

**México.** QUINTANA ROO: Coba, *Lundell 7813* (A, F, MICH). YUCATÁN: Chichén Itzá, *Bequaert 103* (A, F); Valladolid, *Flores 1935* (F); Kancabdzonot, *Gaumer & sons 23894* (A, F); Izabal, *Gaumer 819* (F, GH); Location unspecified, *Gaumer 23976* (F, GH, MICH), *Steggerda 1B* (F); Chichén Itzá, Sacred Cenote, *C.A. & A.A. Lundell 7325* (MICH-holotype; A, F). **British Honduras.** COROZAL DISTRICT: Santa Rita, *Lundell 4951* (A, F, GH, MICH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 560* (DS, F, GH).

*Coccoloba standleyana* Allen, *The Rain Forests of Golfo Dulce* 177, 409. 1956.

The holotype of this species, *Allen 6645*, is in the herbarium of the Escuela Agrícola Panamericana, Tegucigalpa, Honduras. Since the school does not send specimens on loan, I have been unable to study the material; duplicates are not available in other institutions.

*Coccoloba standleyana* is based on sterile material collected in the Esquinas forests of Costa Rica, at an elevation of 200 feet. Allen suggests that the species is "probably related to *C. hirsuta* Standl. and *C. belizensis* Standl. but amply distinct in the much smaller ocreae and other characters." I regard *C. hirsuta* as the same as *C. belizensis* and I suspect that *Coccoloba standleyana* will ultimately be assigned to the synonymy of *C. belizensis*.

*Coccoloba swartzii* Meisner, DC. Prodr. 14: 159. 1856.

*Coccoloba corozalensis* Lundell, Bull. Torrey Club 66: 588. 1939.

*Coccoloba gentlei* Lundell, Bull. Torrey Club 66: 591. 1939.

*Coccoloba swartzii* has not been recognized previously in the flora of Central America, although it is a common element in the vegetation of the West Indies, occurring from Cuba and Jamaica to Curaçao and Aruba and having a great variation in leaf size and shape on all the islands of the Lesser Antilles. The collections cited can be compared favorably with many other collections from the West Indies, especially those populations occurring in the Virgin Islands, the Leeward Islands and the French islands of Guadeloupe and Martinique.

I am not satisfied that the Central American specimens have characteristics of sufficient value to create even a geographical variety. Only the

slightly more tenuous inflorescence axis, with its fewer flowers, appears to differ from the West Indian representatives of the species.

The type of *Coccoloba gentlei* Lundell is *Percy Gentle 56*. The meager material appears to be from a vigorous shoot, perhaps even an adventitious shoot. If considered as the latter, the leaves are comparable to collections I have made on St. Kitts and Montserrat (*R.A. & E.S. Howard 11882, 11867, 11938*). In describing the species Lundell put undue emphasis on the branched inflorescence which in reality is a spike with one anomalous branch developing from the base. This is not an unusual condition either in the genus, or in the West Indian specimens of *C. swartzii*. Standley and Steyermark (*Fiediana Bot. 24: 108. 1946*) place this species in a section of their key with other species having much-branched panicles.

*Coccoloba corozalensis* Lundell is clearly the same as *C. swartzii*.

**British Honduras.** BELIZE DISTRICT: Belize-Sibun Road, *Gentle 56* (MICH-holotype of *C. gentlei*); Pine Ridge, Maskall, *Gentle 1113* (A, F, GH, MICH). COROZAL DISTRICT: Xiabe, *Lundell 4908* (MICH-type of *C. corozalensis*; A, GH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 347* (DS, F). TOLEDO DISTRICT: Monkey Ridge, *Gentle 3651, 3656* (A, MICH). District unspecified: Cornhouse Creek, *Bartlett 11281* (MICH, NY); Mullins River at Stann Creek Road, *Gentle 3359, 3368* (A, MICH). **Honduras.** Point Triunfo, Puerto Sierra, *Wilson 33* (NY).

*Coccoloba tuerckheimii* Donnell Smith, *Bot. Gaz. 37: 213. 1904.*

*Coccoloba guatemalensis* hort. ex Lindau, *Bot. Jahrb. 13: 226. 1890.*

*Coccoloba latifolia* Goyena, *Flora Nicarag. 2: 707. 1911, not Lam.*

According to the collectors' labels, several botanists have believed *Coccoloba tuerckheimii* to be similar to, if not identical with, *C. latifolia* Lamarck from Trinidad and northern South America, although John Donnell Smith made no comparison of these two species in his original description. In a footnote to his monograph of the genus, Lindau assigned cultivated material carrying the unpublished horticultural name *Coccoloba guatemalensis* to *C. latifolia*. I have seen this material which has been attributed to Guatemala and believe it is more correctly referred to the present species than to *C. latifolia*.

*Coccoloba latifolia* is similar to *C. tuerckheimii* in having stout, generally hollow stems, petioles borne slightly above the base of the ocrea, and a paniculate inflorescence. The leaf base is generally rounded or cordate, while the blades are bullate between the veins. In contrast, *C. tuerckheimii* has solid stems with leaf blades tapering to a cuneate base and appearing to be flat. The fruits of *C. tuerckheimii* appear to be larger and more stalked than those of *C. latifolia*.

**Guatemala.** ALTA VERAPAZ: Finca Santa Inés, *Record & Kuylén G-92* (v); Tukurú, *Standley 70724* (F); between Campur and Socoyó, *Standley 91708* (F); Cubilgüitz, *Steyermark 44674* (F), *Tuerckheim 8493* (F-isotype; GH); Cerro, Chinaja, *Steyermark 45568* (F). IZABAL: Río Dulce, Livingston, *Steyermark 39552* (F).

**Honduras.** ATLÁNTIDA: Lancetilla Valley near Tela, *Standley 55812* (A, F);



La Ceiba, *Yuncker, Koepper & Wagner 8603* (F, GH, MICH); Tiquitapa, *Howard, Briggs, et al. 560* (A). YORO: Progreso, *Hottle 92* (F); Subirana, *C. & W. von Hagen 1058* (F). NICARAGUA. CHONTALES: La Libertad, *Standley 9064* (F). COSTA RICA. ALAJUELA: San Carlos, *Suere, A. Smith H-1694* (F, MICH). PANAMÁ. BOCAS DEL TORO: Changuinola Valley, Island of Potrero, *Dunlap 181* (F, Y). COLÓN: Dos Bocas, Río Fato Valley, *Pittier 4197* (F). Cultivated. *Kalbreyer s.n.* as *C. guatemalensis* (B).

***Coccoloba umbilicata* Sessé & Mociño, Fl. Mex. ed. 2. 96. 1894.**

No specimens are cited in the original description in which the species is attributed to Mexico. I have seen the Madrid specimens on loan to the Field Museum, and the sheets labelled "*C. umbilicata*" are all to be referred to *Coccoloba pyrifolia* Desf., a species limited to Puerto Rico.

***Coccoloba uvifera* Linnaeus, Syst. Nat. ed. 10. 1007. 1759.**

*Polygonum uvifera* Linnaeus, Sp. Pl. 365. 1753.

A common strand plant known to all botanical collectors and, as a consequence, one which is poorly represented in herbaria. Presumably the species has a wider distribution in Mexico and Central America than is indicated by the collections cited below.

México. CAMPECHE: Lerma, *Seler 4019* (A, F); Champotón, *Steere 1968* (F, MICH). SINALOA: Mazatlán, *J. Gonzalez Ortega 7203* (BRUX). TAMAULIPAS: Morón, *LeSueur 103* (F); Tampico, *Palmer 477* (F). YUCATÁN: Chichancanab, *Gaumer 1897* (F); Sisal, *Gaumer 23235* (F); Cozumel Island, *Goldman 673* (F), *Millsbaugh 1590* (F); Progreso, *Goldman 603* (F); C.L. & A.A. *Lundell 8060* (MICH); Location unspecified, *Gaumer 638* (F), *Millsbaugh 6* (F). GUATEMALA: IZABAL: Bay of Santo Tomás, *Steyermark 39248* (F, MICH). BRITISH HONDURAS. BELIZE DISTRICT: Turneffe Island, *Egler 42-42* (F); Belize, *Gentle 27* (A, F, MICH). COROZAL DISTRICT: Corozal, *Lundell 4927* (F, MICH). STANN CREEK DISTRICT: Stann Creek, *Gentle 3119* (MICH), *3120* (MICH), *3131* (A, MICH), *3123* (MICH). District unspecified: All Pines, *Schipp 796* (A, F, MICH). EL SALVADOR. LA LIBERTAD: La Libertad, *M.C. Carlson 575* (F). SAN SALVADOR: San Salvador, *Calderón 2624* (F). HONDURAS. ATLÁNTIDA: Tela, *Chickering 51* (MICH), *Standley 53056* (A, F), *Yuncker 4655* (A, F, MICH); Ceiba, *Yuncker, Koepper & Wagner 8235* (F, MICH). COMAYAGUA: Comayagua, *Standley & Chacón 5486* (F). Department unspecified: Puerto Sierra, *P. Wilson 23* (F). SWAN ISLANDS: *Nelson 22* (GH). NICARAGUA. ZELAYA: Bahía de Bluefields, Río Escondito, *A. Molina 1281* (F). COSTA RICA. ALAJUELA: San Roque de Barbe, *León 10* (F). LIMÓN: Limón, Costa de Portete, *Quirós 508* (F); Talamanca, Puerto Viejo, *Tondus 9423* (BRUX). PUNTARENAS: Los Loros and Tivives, *Brenes 22661* (F). PANAMÁ. BOCAS DEL TORO: Almirante, *G. Proctor Cooper 558* (F, Y); Changuinola Valley, *Cooper & Slater 82* (Y); Chiriquí Lagoon, *Von Wedel 2826* (MO). Province unspecified: Isthmus of Chagres, *Fendler 287* (LE, MO).

***Coccoloba venosa* Linnaeus, Syst. Nat. ed. 10. 1007. 1759.**

*Campderia floribunda* Benth. Bot. Sulphur 159. tab. 52. 1846.

*Campderia mexicana* Meisner, DC. Prodr. 14: 171. 1856.

*Coccoloba alagoensis* Weddell var. *major* Meisner, DC. Prodr. 14: 163: 1856.

*Coccoloba floribunda* Lindau, Bot. Jahrb. 13: 217. 1890.

*Coccoloba molinae* Standley & L. Williams, Ceiba 3: 198. 1952.

The synonymy given for *Coccoloba venosa* is new, *C. floribunda* and *C. molinae* and *Campderia mexicana* being reduced here for the first time. An examination of the type specimens alone would make this decision a questionable one, except for *C. molinae* which is clearly the typical West Indian expression of *C. venosa*. Standley and Williams described *C. molinae* in 1952 but were incorrect in believing that their new species was unlike any material then known from southern Central America. In his Flora Nicaragüense (2: 707. 1911), M. Ramírez Goyena recognized *Coccoloba nivea* from Nicaragua and gave the same common name reported for *C. molinae*. *Coccoloba nivea* Jacq. is a synonym of *Coccoloba venosa* L. The specimens which Standley and Williams cite for *C. molinae* are obviously variable, since two phases of coriaceous leaves are shown even in the two specimens of the type number which I have seen. *Coccoloba molinae* is undoubtedly the same as *C. venosa* L.

*Coccoloba floribunda* described by Bentham was based on material collected on the voyage of the Sulphur. The type came from Tiger Island in the Gulf of Fonseca, Honduras. *Campderia mexicana* was based on Andrieux 115, a specimen from Tehuantepec, Oaxaca, Mexico, and since there is no difference between these, Lindau placed *Campderia mexicana* in synonymy. Recent collections from the same area are also cited.

*Coccoloba floribunda* as defined by Lindau and as generally recognized in current floras is strikingly different from *C. venosa* as generally recognized in the West Indies. In drier areas the leaves are thick and almost rigidly coriaceous. The leaf apex is obtuse, rounded or even truncate and the base slightly narrowed but rounded or obtuse. Bentham described the leaf base as emarginate to slightly peltate, although the type specimen and the illustration fail to show the latter condition. The leaves are much smaller and the inflorescence generally shorter and thicker than *C. venosa*. At greater altitudes and in wetter areas, according to the data on the specimens studied, the differences are less obvious between *C. floribunda* and *C. venosa*. The leaves become thinner, longer, the apex pointed, the inflorescence axis longer and more tenuous in comparison.

A full range of variation between the extremes has been found in the specimens cited below to indicate a variable population over the geographic range of the species. I have been unable to find any stable characteristics which would allow the segregation of the smaller, coriaceous-leaved form as a geographic variety. Lindau separated *C. floribunda* from *C. venosa* (his *C. excoriata*) in a key to the species (Bot. Jahrb. 13: 130. 1890) by placing *C. floribunda* in a group in which the leaves are more or less pubescent below or at least barbellate in the vein axils, while *C. venosa* reportedly had glabrous leaves. Comparable pubescence along the midrib and in the axils of the veins is found in the West Indian specimens, so Lindau's distinction does not hold.

Additional study of this species in the field is needed to establish leaf shape, size and texture variations on single plants in Central America, espe-



cially since none of the collections I have seen represents adventitious or fast-growing shoots. In their treatment of *Coccoloba floribunda* for the Flora of Guatemala (Fieldiana Bot. 24: 113. 1946), Standley and Steyermark described the species as "a densely branched shrub or tree, sometimes 9 meters high, with a broad spreading crown, the low trunk often gnarled and twisted, sometimes a meter in diameter." This description fits well many of the plants seen in the Antilles. Variations in leaf texture from membranaceous and chartaceous to coriaceous have also been encountered in *C. venosa* in the Lesser Antilles, although a reduction in leaf size or an adjustment of shape comparable to that found in many of the specimens cited has not been encountered.

Among the specimens cited is *Standley 74249* from Guatemala, represented by two sheets from two different locations.

*Coccoloba venosa* is under cultivation in Cuba and has been reported from Jamaica in old literature, but no specimens referable to the island have been seen. It is common in Hispaniola, Puerto Rico and the Virgin Islands south through the Lesser Antilles to Trinidad. I have also seen two collections from Venezuela.

**México.** CHIAPAS: Belem, Mapastepec, *Matuda 16741* (F, GH); Tapachula, *Fisher 35437* (F, NY); Huixtla, *Matuda 16795* (F); Las Garzas, Acapetagua, *Matuda 2683* (A, F, MICH); Mojarra, Tonalá, *Matuda 17125* (F). COLIMA: Manzanillo, *Ferris 6057* (DS), *6245* (A, DS). GUERRERO: Acapulco, *MacDaniels 199* (F, MICH). JALISCO: Mazatlán, *Liebmann s.n.* (B). OAXACA: Salina Cruz, *Deam 121* (GH, MICH), *L. I. Williams 9708* (F, MICH); Tehuantepec, *Zuccarini s.n.* (M). Province unspecified: *Haenke 1608* (F); *Sessé & Mocino 5432*, *5435* (F).

**Guatemala.** CHIQUIMULA: Quebrada Shusho above Chiquimula, *Standley 74249* (F). GUATEMALA: Location unspecified, *Aguilar 550* (F). JUTIAPA: Jutiapa, *Standley 75193* (F, MICH). RETALHULEU: Champerico, *Bernoulli & Cario 2663* (LE), *Standley 66507* (A, F), *87547* (F, MICH). SANTA ROSA: between Chiquimulilla & El Ahumado, *Standley 79541* (F). ZACAPA: Zacapa, *Standley 74249* (F); *74379* (F, MICH); Río Motagua west of Teculután, *Steyermark 29195*, *42167* (F). Department unspecified: Location unspecified, *Friedrichsthal s.n.* (MICH-type of *C. alagoensis* var. *major*; F).

**El Salvador.** LA LIBERTAD: La Libertad, *Standley 23231* (GH, US), *Calderón 2399* (F). LA UNIÓN: La Unión, *Grant 722* (A, F), *Standley 20644* (GH). SAN MIGUEL: Laguna de Olomega, *Standley 21015* (GH); San Miguel, *Standley 21133* (GH). SAN SALVADOR: Hacienda Santo Tomás, *Carlson 1124* (F). SANTA ANA: Metapán, *Standley & Padilla 3297* (F). SONSONATE: Acajutla, *Calderón 1662* (GH, US); Izalco, *Standley 21861* (GH, US). Department unspecified: location unspecified, *Choussy 2054* (US).

**Honduras.** VALLE: San Lorenzo, *Rodriguez 3299* (F); Isla Tigre, near Amapala, *Standley 20728* (GH, US); El Tigre volcano above Amapala, *West 3534* (GH); Jicaro Galán, *Williams & Molina 15002* (F); Nacaome, *Williams & Molina 16721* (F).

**Nicaragua.** Chinandega: Corinto, *Standley 11545* (F). CHONTALES: Juigalpa, *Standley 9220* (F). GRANADA: Granada, *Baker 203* (DS, GH), *Lévy 1352* (F). MANAGUA: Managua, *Garnier 320* (W); Sierras de Managua, *Grant 1097* (A, F).

ZELAYA: Río Grande, *Molina* 2291 (F, GH); Toumarin, Río Grande, *Molina* 2436 (F-isotype; GH); El Recreo on Río Mico, *Standley* 19600 (F). Department unspecified: Asseradores Island, *Baker* 81 (DS, GH); Location unspecified, *Lévy* 1103 (B), *Wright s.n.* (GH, NY).

**Costa Rica.** GUANACASTE: Libano, *Standley & Valerio* 44900 (F). NICOYA: Nicoya, *Tonduz* 13779 (F, GH, MICH). PUNTARENAS: Los Loros, *Brenes* 22470 (F); between Los Loros & Tivives, *Brenes* 22680 (F); Caldera, *Echeverria* 4155 (F); Isla de Chira, *Orozco* 233 (F); *Valerio* 1466 (F).



## THE POLLEN OF EPHEDRA

MARGARET WOLFE STEEVES AND ELSO S. BARGHOORN

THE ORIGIN OF THE GNETALES and their relationship to other fossil and living gymnosperms is a problem which is nearly as baffling as that of the origin of the flowering plants; and indeed the two problems have often been linked. On the study of the Gnetales, paleontology has contributed very little because of the extreme paucity of fossil remains (Pearson, 1929). Consequently any early fossil material of this group, and particularly of the most primitive member, *Ephedra*, may be regarded with great interest by students of plant evolution. The first reference to fossil remains of this gnetalian genus is found in *Die im Bernstein befindlichen organischen Reste der Vorwelt*, a description of the Oligocene Baltic Amber flora (Berendt and Göppert, 1845). In their study, twigs bearing ovuliferous structures were designated *Ephedrites johnianus*. A translation of their Latin description is as follows:

Stem jointed, joints cylindrical with longitudinal striations ending in an annular sheath.

Aments subglobose, single, composed of imbricated bracts, and elevated on the apex of thickened peduncles. The peduncles are verticillate, in the axis of the sheath and non-articulate.

As a result of Menge's subsequent discovery of a preserved male strobilus from the same flora and further study of Göppert and Menge's material, the close similarity between the fossil remains and modern *Ephedra* became apparent. For this reason the genus was redescribed as *Ephedra* (Göppert, 1853; Göppert and Menge, 1883).

Later workers have described *Ephedra* fragments from the Miocene of Germany and Switzerland (Unger, 1851, 1870), and the Miocene of France (Saporta, 1889, cited by Wodehouse, 1934) but there has been some dispute concerning the validity of these identifications. Heer (1855), in publishing a report of *Ephedrites sotzkianus* Unger in his *Flora Tertiaria Helvetiae*, conceded that there was a superficial similarity between these articulate, striated, fossil stems and those of *Casuarina*, an isolated, Australian genus of angiosperms. However, Schimper (1890) saw no similarity with the genus *Casuarina* but questioned all previous reports of the genus from the Tertiary on the grounds that they could belong to poorly preserved specimens of either *Equisetum* or the conifer *Callitris*.

As a result of this confusion it was not until the application of pollen analysis to older sediments that remains of *Ephedra* were uncontestedly demonstrated in the Tertiary. Furthermore, with the discovery of *Ephedra* pollen by Wodehouse from the Green River Formation (1933), the past geographic distribution of the genus was broadened to include North America. Likewise, its geologic record was extended back to the Eocene.

Although Tertiary and Pleistocene records in the Western Hemisphere have become more complete with the discoveries of megascopic remains of *Ephedra* from the Florissant beds of Colorado (Wodehouse, 1934), the Pleistocene of California (Axelrod, 1937), the Pleistocene of Nevada and Arizona (Laudermilk and Munz, 1934, 1938), micropaleontological evidence has been surprisingly rare both in Europe and the United States. Thiergart (1940) reported the presence of fossil *Ephedra* pollen grains from Tertiary beds in Germany, Cookson (1956) has recorded them from Australian Tertiary sediments, and, as a result of recent pollen studies, it has been shown that *Ephedra* persisted as a late- and postglacial desert steppe plant in protected areas in Europe (Christensen, 1949, cited by Iversen, 1954; Lang, 1951; Iversen, 1954; Welten, 1957) as well as in South America (Auer, 1933) and the United States (Anderson, 1954).

In view of the facts that *Ephedra* possesses a high degree of structural specialization, and also that early Tertiary *Ephedra* exhibits pollen structures essentially comparable with that of modern species it is apparent that the genus or its close ancestral type had an extended pre-Tertiary history. An extension of this pre-Tertiary history has been found during an analysis of a series of cores from the Cretaceous Raritan and Magothy formations from east-central Long Island, New York. In these sediments a number of intact, as well as fragmented, pollen grains assignable to *Ephedra* were observed. This discovery extends the known fossil record of the genus in North America back to the lower Upper Cretaceous period.

The first part of this paper will deal with a description of the fossil grains found on Long Island; in the second part the results of a detailed survey of the pollen morphology of the living members of the genus will be presented with a view to interpreting the fossil forms and their phylogenetic significance.

#### FOSSIL EPHEDRA FROM CRETACEOUS SEDIMENTS OF LONG ISLAND

In the process of exploratory sub-surface geologic studies at the Brookhaven National Laboratory, two deep well cores were recovered from two borings approximately one mile apart. The cores extended from the surface Pleistocene drift through the Cretaceous and into the underlying bedrock. The cores were recovered nearly intact and represent an unusually complete section of the Cretaceous formations underlying eastern Long Island. One of us had the opportunity to sample both of these cores throughout, and this study comprises one aspect of an intensive micropaleontological study still in progress.<sup>1</sup>

The cores, designated Well No. 1 (S 6409) and Well No. 2 (S 6434) were drilled to a depth of 1,568 feet and 1,294 feet, respectively. In both

<sup>1</sup> Samples of the cores were made available in May 1950 by the Ground Waters Division of the U. S. Geological Survey and were transmitted through the courtesy of the Paleontology and Stratigraphy Branch of the Geologic Division of the U. S. Geological Survey.



cores, which were drilled through the Magothy and Raritan formations, the sediments recovered were all non-marine, Coastal Plain deposits, comprising variegated and lignitic clays, white, fine-grained and coarse arkosic sands, and gravels. Occasional lignite beds were dispersed throughout the section. The entire sequence rested on crystalline igneous rocks of presumed pre-Cambrian age.

The Magothy formation is regarded as of Upper Cretaceous age and has been correlated with the Austin chalk of the Gulf Coast region. Although it rests unconformably on the Raritan, rarely is the Magothy clearly differentiated from it. According to Spangler and Peterson (1950), the two formations are comparatively easy to differentiate in the field but insufficient contacts of the two have been found to map them satisfactorily. Data available from well logs are usually too uncritical and incomplete for stratigraphic purposes. The Raritan formation of New Jersey was considered by Spangler and Peterson (1950) as equivalent to those non-marine sediments in Delaware, Maryland and Virginia referred to as "Raritan," Patapsco, Arundel and Patuxent. This series, they believe, should be considered as a single unit and comprises both Upper and Lower Cretaceous beds. Furthermore, the beds called "Raritan" in Maryland-Delaware are only part of the sediments called Raritan in New Jersey. However, they point out that the contact of the Upper and Lower Cretaceous occurring within the Raritan formation in New Jersey has not been recognized in outcrop and sub-surface sediments have not been studied. This interpretation has been refuted by Dorf (1952) who, after reviewing the faunal and floral evidence, reaffirmed the assignment of the Raritan formation to the early Upper Cretaceous. Hence, in his view, the Potomac beds (Arundel, Patapsco and Patuxent) are pre-Raritan and assignable to the Lower Cretaceous. One of the purposes of this study was to examine the possibility of separating the Raritan from the Magothy on the basis of evidence from plant microfossils. Such a separation might render stratigraphic correlation possible in other parts of the Coastal Plain where the two formations are at present unsatisfactorily separable.

Small samples (1-2 gms.) taken at intervals along the length of both cores were prepared according to techniques modified from Erdtman (1943), Faegri and Iversen (1950). The material was first demineralized by a treatment of cold 50% HF for 24-48 hours, then boiled in 10% KOH in a water bath for six minutes, washed, and dehydrated with glacial acetic acid. The remaining cellulose was removed by acetylation for 1½ minutes at 100° C. By this sequence of chemical treatments such constituents as quartz and clay minerals, lignin and cellulose are removed and the cutinized and suberized pollen grains and spores are concentrated.

In our material, evidence for the existence of a species of *Ephedra* was provided by the presence of ridged pollen grains found at the 603-613 foot level of Well No. 2. To these grains, which could be related to modern forms of *Ephedra*, the designation "Type A" was given.<sup>2</sup>

<sup>2</sup> This terminology is based on a study of modern *Ephedra* and will be clarified in the second part of this paper.

A total of eight intact grains of Type A and a number of fragments of similar type were found. A list of the intact fossil grains and their measurements is shown in TABLE I.

The Type A grains are prolate, their shape class index<sup>3</sup> varies from 1.5 to 1.9, the average being 1.7. The polar axis measures 47–53  $\mu$ , the average being 49  $\mu$ ; the equatorial diameter varies from 26–33  $\mu$ , the average being 29  $\mu$ .

TABLE I. A list of the fossil grains and their measurements.

<i>Ephedra</i>	LOCATION	SIZE	NUMBER OF RIDGES	S.C.I.*
A 1	45–85.5 (S1)	47 $\times$ 29 $\mu$	5	1.6
A 2	45–85.5 (S1)	49 $\times$ 26 $\mu$	6	1.9
A 3	39.8–88 (S3)	53 $\times$ 33 $\mu$	6	1.6
A 4	27.5–88 (S2)	47 $\times$ 30 $\mu$	6	1.5
A 5	41–97 (S2)	dia. 32 $\mu$	6	
A 6	37.5–103 (S1)	50 $\times$ 27 $\mu$	6	1.8
A 7	40–87.5 (S1)	53 $\times$ 29 $\mu$	6	1.9
A 8	42–95.5 (S1)	47 $\times$ 30 $\mu$	6	1.5
Average		49 $\times$ 29 $\mu$	6	1.7

\* Shape class index.

Characteristic features of these pollen grains are the narrow, undulating ridges which extend meridionally from pole to pole. These ridges fuse at the poles so that there are actually three continuous, intersecting ridges circumscribing the grain.

The exine is double and intectate. It consists of a thick endexine and a highly variable ectexine. In thickness the endexine is constant, averaging between 0.5 and 1  $\mu$  over the entire surface of the grain. However, the ectexine fluctuates considerably in thickness, averaging 0.5–1  $\mu$  along the region between the ridges and 3–4  $\mu$  at the central peak of the ridge at the equator. Furthermore, ridge height increases poleward to 4–5  $\mu$  as a result of the fusion of the ridges.

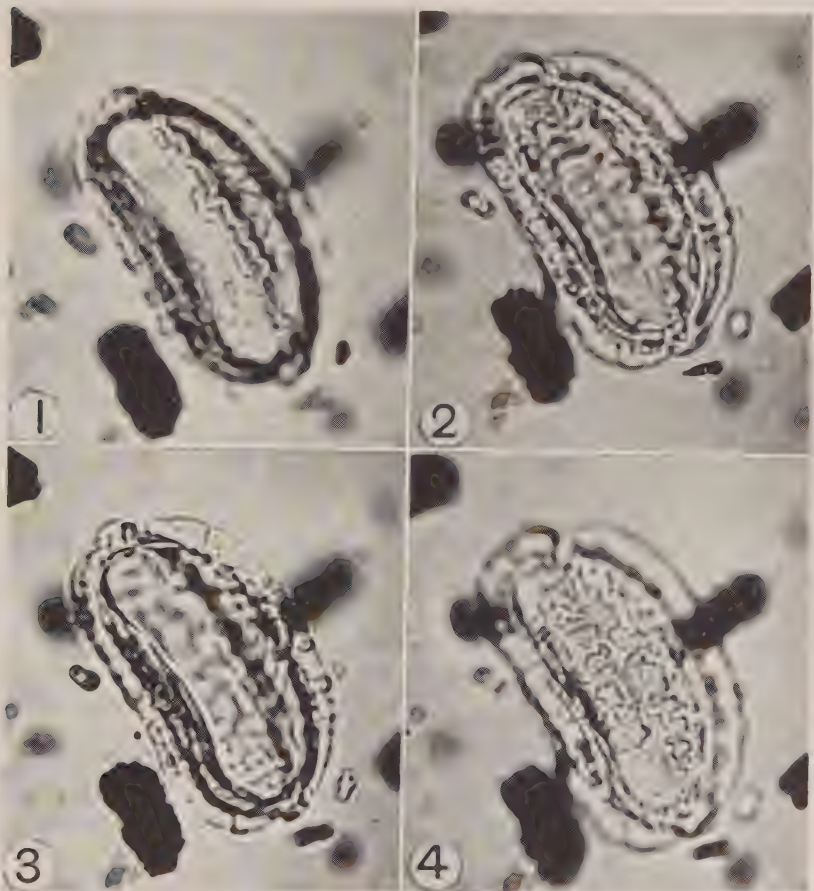
In surface view, the highly undulate wave-like pattern of the ridge is evident. The wave height measures 2–3  $\mu$  and the wave length averages 2–4  $\mu$ . In the majority of cases the ridges are continuous. However, in a few cases the ridges are composed of short, individual, angular undulations which overlap one another but are not fused. In width, the ridges average between 0.8  $\mu$  and 1.5  $\mu$  at the equator becoming thinner at the poles. With high magnification two slender, hyaline lines, averaging less than half a micron in width can be seen to run along the surface of each ridge bordering its edge. A central strip 0.2  $\mu$  wide, which remains dark, separates these two undulate and highly refractive borders. With changing focal levels a reversal of the light–dark relationship of the central strip and

<sup>3</sup> Shape class index is the ratio of the long axis to the short axis (Erdtman, 1943).



the bordering lines is produced, so that the central strip appears as a single hyaline line.

In optical section, the ridges appear to be composed of individual baculate projections which extend out from the grain at right angles to the endexine. However, these are not true baculae, which are defined by Faegri and Iversen (1950) as "radial projections with the height of the element greater than the greatest diameter of projection and the upper end of the element not thicker than the base." Rather, the projections represent profile views of the ridge which is seen optically sectioned at various angles as a consequence of its highly irregular form.



TEXT-FIGURE 1. *Ephedra stapfi* Steeves & Barghoorn, n. sp. 1, High focus view of the undulating ridge. 2, Same grain at mid-focus, showing the outline of the distinct, thick endexine. 3, A view slightly beyond mid-focus showing the thickness as well as the baculate appearance of the ectexine in optical section. 4, High focus view of the reticulate sculpturing found on the surface of the exine between the ridge crests on the opposite side of the grain. (All  $\times 1000$ .)

The grains as a whole appear slightly angular in polar aspect with the ridges forming the angles. In this view the ridges themselves appear rounded and slightly constricted at their bases.

The surface sculpturing of the grain is rugulate-reticulate with muri 0.8–1  $\mu$  wide and 0.5  $\mu$  high extending out from the ridge crest down the ridge flanks enclosing lumina 2–4  $\mu$  in diameter.

*Ephedra stapfii*, n. sp.

TEXT-FIGURE I.

DIAGNOSIS: Grains prolate, the polar axis varying from 47 to 53  $\mu$ , averaging 49  $\mu$ ; equatorial diameter varying from 26 to 33  $\mu$ , averaging 29  $\mu$ . Ridges 5 or 6, highly undulate, extending from pole to pole. Shape class index varying from 1.5 to 1.9, averaging 1.7.

LOCALITY: Brookhaven, Long Island, New York; U.S.G.S. Well No. 2, 603–613-foot level.

GEOLOGIC OCCURRENCE: Raritan formation, lower Upper Cretaceous.

MATERIAL: Eight intact pollen grains and a number of fragments.

HOLOTYPE: No. 56011, Palaeobotanical Collections, Harvard University.

POLLEN MORPHOLOGY OF MODERN SPECIES OF EPHEDRA

Stimulated by the discovery of ephedroid pollen of considerable geologic age, an intensive study was made of the pollen of existing species of *Ephedra* with a view to determining the possible phylogenetic significance of the fossils.

Modern *Ephedra* pollen was first described extensively by Wodehouse (1935), who recognized basic differences within the genus based on his work with *E. equisetina* and *E. foliata*. In his description of *E. equisetina* he states that the pollen is characterized by having "high few ridges 5–8 with their crests blade like and arching from end to end of the grain, and in each of the grooves between the ridges is a hyaline line which follows a serpentine course its full length." A description of *E. foliata* notes that "when the ridges are more numerous, 11 to 15, they are not so high and the hyaline lines in the grooves are absent or only represented by a faint streak." His descriptions of these two species represent a few of the many variations in form that characterize pollen of the genus. Although the grains are all similar in their possession of ridges, they differ in size, in shape, in number of furrows and ridges and in exine structure. Recently, Welten (1957) studied extensively the species of the Mediterranean and western Asian regions in order to identify pollen of *Ephedra* from northern and central European late- and postglacial sediments.

Although the taxonomic treatment of the genus is somewhat unsatisfactory, forty-three of the currently recognized forty-eight species of *Ephedra* were examined in the present study. A list of the species, as well as their geographic source, is given in TABLE II. In the course of the work it became apparent that the pollen of *Ephedra* falls into certain major morphological categories. These we have arbitrarily designated A, B, C, and D. The characteristics of the four designated pollen types will be con-

sidered in detail as illustrated by descriptions of individual species. It would be of much interest to examine the relationship of these divisions, based on pollen morphology with those based on other organs and parts of the plant. Although such information is not available on a wide range of species it would add to the phylogenetic significance of the fossil forms.

#### POLLEN TYPE A

The grains are perprolate to subprolate in shape, their shape class index varying from 1.1 to 2.6 but generally averaging 1.8. The grains are sculptured by an average of 5 to 9 heavy, hyaline, ektexinous ridges which extend meridionally from pole to pole. The least amount of variation is observed in *Ephedra sinica* where the ridge number ranges between 4 and 6 and averages 5.8. The greatest number is found in *E. pachyclada* and *E. funera*. In the former species the ridge number varies from 5 to 12 and averages 7.9, in the latter it ranges from 6 to 13 and averages 8.3. (See CHART II which is based on an average of 50 grains per species.)

In the polar view the grains are polygonal with the alternating ridges and deep concave furrows forming an angular outline. A narrow and serpentine colpus<sup>4</sup> is situated at the base of each furrow. In most cases the colpi are highly undulate. The undulation of the colpus may be either rounded or highly angular and the frequency of undulation may vary, as well as the degree. The colpus may divide forming lateral branches which extend up the ridge where they may occasionally divide again. In this manner the ektexine forms a reticulate pattern, such as that found in *E. distachya*. In a few cases, as in *E. clokeyi*, the colpus scarcely divides. Also, the width of the colpus may vary, as well as the depth to which it cuts into the ektexine.

The ridge itself may be relatively smooth or highly verrucate. The term "verrucate" in the manner in which it is used here may be open to question but it is chosen for the sake of simplicity. The true "verruca" has been defined as a sculpturing element in which "the greatest diameter of the radial projection is greater than the height of the element" (Faegri and Iversen, 1950). In *Ephedra* pollen, however, the ridge crest appears verrucate in optical section because of the cutting of the ektexine by the branching colpi which extend up the ridge. In all species possessing Type A pollen, except *E. sinica*, the ridges are triangular in shape in the polar aspect with bases which vary in width from 0.5 to 18  $\mu$  and central axes which range in height from 3 to 8  $\mu$ . As was recognized by Welten (1957), the ridge in this view is composed of an inner, central, hyaline core and a thin,

<sup>4</sup> Colpus (pl. colpi), germinating furrow, the area on the grain forming or surrounding the normal place of emergence of the pollen tube, with a length-breadth ratio higher than 2. The ektexine is reduced, even absent (Faegri and Iversen, 1950; Ingwersen, 1954). Although the terms furrow and colpus may be used interchangeably, in this case a distinction between the two will be made. The term "furrow" will be used to refer to the region between the ridges; the term "colpus" will be used to describe the thin, longitudinal, serpentine grooves located in the middle of the furrow area and formed by the absence of or the thinning of the ektexine.



TABLE II. Species of *Ephedra* examined in this study.\*

SPECIES	SOURCE	COLLECTION
<i>Ephedra alata</i> Dcne.	Algeria	Bornmüller (A)
<i>E. altissima</i> Desf. var. <i>mauritanica</i> Stapf	Morocco	Balls 2487 (A)
<i>E. americana</i> Humb. & Bonpl. ex. Willd.	Bolivia	Cardenas 3422 (GH)
<i>E. andina</i> Poepp. & Endl.	Chile	Joffuel 2751 (GH)
<i>E. antisiphilitica</i> Ber- land	W. Texas	<i>E. Palmer</i> 1292 (GH)
<i>E. aspera</i> Engelm. ex. S. Wats.	New Mexico	Wright 1851 (GH)
<i>E. bracteata</i> Miers	Chile	Jegons (GH)
<i>E. breana</i> Phil.	Prov. Antofagasta, Chile	Johnston 3613 (GH)
<i>E. californica</i> S. Wats.	San Diego Co., California	Epling (GH)
<i>E. chilensis</i> Miers	Valparaiso, Chile	Goodspeed 4592 (GH)
<i>E. clokeyi</i> Cutler	Washington Co., Utah	Gould 1526 (GH)
<i>E. coryi</i> Reed var. <i>vis-</i> <i>cida</i> Cutler	Rock Point, Arizona	Cutler 2768 (GH)
<i>E. distachya</i> L.	Germany	Flora Germanica Exsic- catae 7513 (GH)
<i>E. equisetina</i> Bge.	Turkestan	Korshinsky, Herb. Inst. Bot. Ac. Sc. USSR 6384 (A)
<i>E. foliata</i> Boiss. & Kot- schy ex. Boiss.	Punjab, India	Parker 3304 (A)
<i>E. foliata</i> Boiss. var. <i>ciliata</i> (C.A.Mey.) Stapf		Aitchison 537 (GH)
<i>E. fragilis</i> Desf.	Prov. Almeria, Spain	Reverchon 611 (A)
<i>E. fragilis</i> Desf. var. <i>campylopoda</i> (C.A. Mey.) Stapf	Palaestine	Bornmüller 1746 (A)
<i>E. frustillata</i> Miers	Rio Negro, Argentina	Parodi 11858 (GH)
<i>E. funera</i> Cov. & Mort.	California	Hitchcock 329 (GH)
<i>E. gerardiana</i> Wall.	Kashmir	G. L. Webster 5830
<i>E. gracilis</i> Phil.	Prov. Atacama, Chile	Johnston 6208 (GH)
<i>E. graeca</i> C. A. Mey.	Morocco	Baumier (GH)
<i>E. helvetica</i> C. A. Mey.	Switzerland	Reliquiae Mailleanae 7046 (GH)
<i>E. intermedia</i> Schrenk & C. A. Mey. var. <i>schrenkii</i> Stapf	Teheran	Bornmüller (A) det. Florin
<i>E. major</i> Host var. <i>procera</i> Aschers. & Graebn.	Talas Ala-Tau branch of the Tien-Shan Mountains in N. W. Kirghiz USSR.	Herb. Hort. (A) Bot. Univ. Asiae Mediae

\* Pollen obtained from herbarium specimens in the herbarium of the Arnold Arboretum (A) and the Gray Herbarium (GH). The dried herbarium pollen grains were acetylyzed for one and one-half minutes in boiling water, washed in three changes of distilled water and mounted in glycerine jelly.

SPECIES	SOURCE	COLLECTION
<i>E. major</i> Host var. <i>villarsii</i> Stapf	Amasya, Turkey	Bornmüller 3544 (A)
<i>E. monostachya</i> L.	Saknain-Nor, Tibet	— (A)
<i>E. multiflora</i> Phil. ex. Stapf	Argentina	Johnston 6286 (GH)
<i>E. nana</i> Dusen	Patagonia	Donat 42 (GH)
<i>E. nevadensis</i> S. Wats.	New Mexico	Tower (GH)
<i>E. ochreate</i> Miers	Argentina	Fisher 15 (GH)
<i>E. pachyclada</i> Boiss.	Afghanistan	Aitchison 1122 (GH)
<i>E. pedunculata</i> Engelm. ex. S. Wats.	Mexico	Stewart 2265 (GH)
<i>E. peninsularis</i> I. M. Johnston	Mexico	Anthony 281 (GH)
<i>E. regeliana</i> Florin	Skardu, Baltistan	G. L. Webster 5950
<i>E. rupestris</i> Benth.	Bolivia	— (GH)
<i>E. sinica</i> Stapf	Prov. Suiyuam, China	Licewtak 13523 (A)
<i>E. strobilacea</i> Bge.	Turkmenistan, USSR	Herb. Inst. Bot. Ac. Sc. USSR (A)
<i>E. triandra</i> Tul.	Bolivia	Fiebrig 2151 (GH)
<i>E. trifurca</i> Torr.	New Mexico	Hortman 642 (GH)
<i>E. torreyana</i> S. Wats.	Rocky Mt. Region, Uinta Co., Utah	Rollins 1719 (GH)
<i>E. tweediana</i> Fisch. & C. A. Mey.	Uruguay	— 5683 (GH)
<i>E. wraithiana</i> I. M. Johnston	Chile	Johnston 4705 (GH)
<i>E. viridis</i> Cov.	Mt. Pinos, Kunto, California	Howell 3824 (GH)
<i>E. vulgaris</i> C. A. Mey.	Magnesia, Greece	Aitchison 40 (GH)

outer, non-hyaline layer. The ridge peak is not pointed, but rounded, and averages 1.5 to 4  $\mu$  in width. The ridges tend to decrease slightly in height at the poles and the verrucae gradually disappear.

The exine is always double and may measure up to a maximum of 8  $\mu$  in thickness. It is composed of a relatively thin endexine which extends continuously and evenly around the grain, varying in thickness from 0.8 to 2  $\mu$ , and an ectexine which averages 1 to 2.5  $\mu$  in thickness in the furrow region and 3 to 6  $\mu$  along the central axis of the ridge. The ectexine is double. One component, the inner, hyaline layer forms the triangularly shaped central core of the ridge. This layer extends completely around the grain becoming thinnest at the colpi and accounts for the hyaline appearance of the colpi at some levels of focus. The thinner, outer layer is continuous or discontinuous, depending upon the depth of the colpi.

The group as a whole ranges in size along the polar axis from 51  $\mu$ , the average in *E. vulgaris*, to 69  $\mu$ , the average in *E. funera*, with considerable overlap between species. To a certain extent a distinction between species with large pollen and species with small pollen in the Type A group can be

CHART I

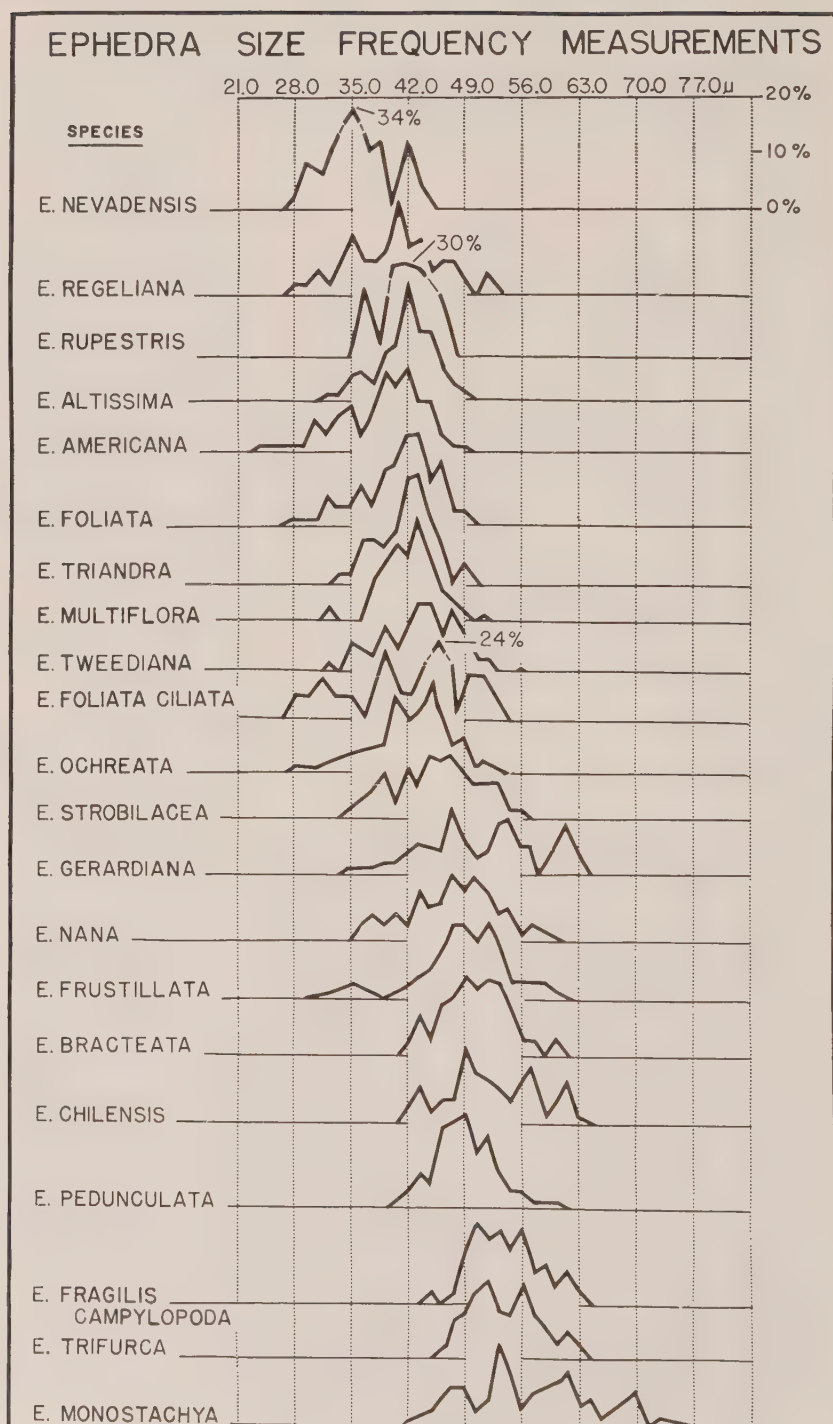
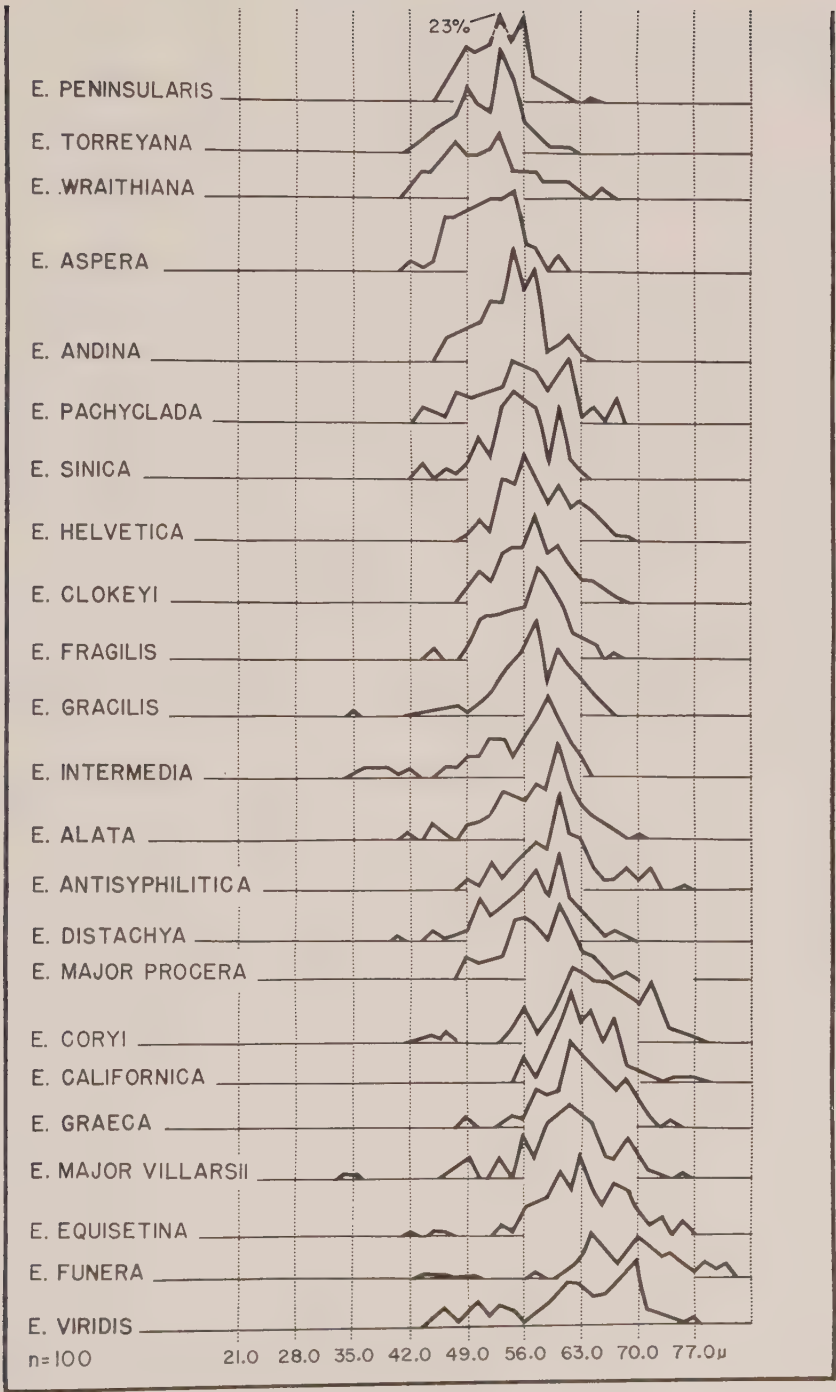




CHART I (Continued)



made, although the variability in size within the species limits the taxonomic usefulness of this character (CHART I).

#### DESCRIPTION OF SPECIES OF TYPE A

##### *Ephedra distachya* L.

PLATE I, fig. 3; PLATE II, figs. 1, 2.

Polar axis  $56\ \mu$  ( $40\text{--}66.5\ \mu$ ); equatorial diameter  $30.5\ \mu$  ( $24\text{--}36\ \mu$ ). Ridges  $6.4$  ( $4\text{--}9$ ). Shape class index  $1.8$  ( $1.4\text{--}2.1$ ); prolate.

Viewed in the equatorial plane, the grains are prolate, their shape class index averaging  $1.8$  and lying between  $1.4$  and  $2.1$ , whereas in their polar aspect they are polygonal. The furrows are deep, with concave sides and narrow, serpentine colpi situated at their bases. The grains could be termed polycolpate, possessing  $4\text{--}9$  undulating colpi which extend between the poles. The undulations are acutely angular and occur every  $2\text{--}6\ \mu$ . The colpi average  $0.8\ \mu$  in width and are formed by a complete absence of ectexine in that region. The colpate condition (according to Wodehouse, 1935) permits harmomegathic contraction and expansion along the equatorial axis of the grain where the exine is thinnest or absent. The colpi are bordered by a verrucate ridge  $5\text{--}6\ \mu$  high, the verrucae measuring  $2\text{--}4\ \mu$  in length and  $2\text{--}3\ \mu$  in width. In optical section the individual verrucae appear semicircular in shape with slightly flattened edges. The colpi merge but do not fuse at the poles, terminating just previous to it; the ridges fuse at the poles. At the equator the ridges average  $5\text{--}7.5\ \mu$  in width at the base and  $2.5\text{--}3\ \mu$  at the crest. Their height ranges from  $5\text{--}6\ \mu$  at the equator to  $1.5\ \mu$  at the poles.

The ectexine is variable in thickness, measuring  $3\text{--}4\ \mu$  along the ridge peak at the equator, decreasing toward the poles where it is  $1.5\text{--}2\ \mu$ , as well as toward the colpi where it is probably absent. The endexine is thinner than the ectexine, measuring  $1\ \mu$  or less and is continuous. The structure of the exine is intectate. In surface view within the furrow a coarse, reticulate sculpturing of the ectexine is visible. However, this is an inverted reticulum in the sense that the exine is not divided into lumina by the presence of walls or muri but rather by thin, narrow indentations derived from short, lateral branches of the main, longitudinal colpus. This branching occurs only at the angles formed by the undulations of the colpus (Faegri and Iversen, 1950, use the term fossulate to describe an exine dissected in this manner). These lateral branches are set off  $2.5\text{--}6.5\ \mu$  apart along the course of the main colpus, and may dichotomize again and continue up the ridge to the crest, deeply cutting the thick exine into angular, closely set verrucae.

##### *Ephedra clokeyi* Cutler

Polar axis  $56\ \mu$  ( $47\text{--}68\ \mu$ ); equatorial diameter  $31\ \mu$  ( $27\text{--}41\ \mu$ ). Ridges  $7.2$  ( $6\text{--}9$ ). Shape class index  $1.6$  ( $1.4\text{--}2.1$ ); prolate.

Similar to the *Ephedra distachya* type but differing in the possession of a markedly smoother exine, the ridge flanks of this species are not cut by branching, lateral colpi, which in the other species of the A type extend

from the main colpus up the ridge to its crest. The ridge crest, however, is slightly crenulate. Moreover, the ridge is highly irregular with undulations measuring 8–12  $\mu$  in length and 2.5–3  $\mu$  in height. At the equator the ridges average 7  $\mu$  in width at the base and 2  $\mu$  at the crest; the colpi are narrow, straight or only slightly undulate and average 0.3  $\mu$  in depth.

Thickness of the ectexine at the ridge crest at the equator 2.5–3  $\mu$ , at the poles 2  $\mu$ , in the furrow area 0.8–1  $\mu$ ; thickness of the endexine 1  $\mu$ .

### *Ephedra coryi* Reed var. *viscida* Cutler

Polar axis 63  $\mu$  (43.5–76.5  $\mu$ ); equatorial diameter 31  $\mu$  (28–42  $\mu$ ). Ridges 6.9 (4–9). Shape class index 2.0 (1.5–2.6); prolate-perprolate.

Although similar to those of *Ephedra distachya* in general structure, the grains differ in the possession of a thicker exine and in the shallowness of the lateral branches of the colpi. The thickness of the ectexine varies from 4.5–6  $\mu$  at the center of the ridge at the equator and decreases to 3  $\mu$  at the poles; in the region of the furrow it measures 0.8–1  $\mu$ . The endexine averages 1.6  $\mu$  in thickness. Unlike those found in *E. distachya* the verrucae are semicircular in optical section, widely spaced and project well above the surface of the grain, averaging 4–6  $\mu$  in length. Often the ridge crest itself is undulant.

The colpi average 0.5  $\mu$  in width and follow a very slightly angular path to the poles. Lateral branching occurs every 4–6  $\mu$ ; secondary branching seldom occurs. The depth to which these secondary branches cut into the ectexine along the ridge crest averages 0.5  $\mu$ . At the equator the ridges average 10–11  $\mu$  in width at the base and 2–3  $\mu$  at the crest.

### *Ephedra equisetina* Bunge

Polar axis 56  $\mu$  (39–66.5  $\mu$ ); equatorial diameter 30.5  $\mu$  (23–36  $\mu$ ). Ridges 5.9 (4–8). Shape class index 1.9 (1.4–2.1); prolate.

The grains, more delicate than the preceding species, have thin exines composed of ectexines measuring 1.5  $\mu$  at the ridge crests at the equator and endexines averaging 0.8–1  $\mu$  in thickness. At the poles and in the furrow region the thickness of the ectexine diminishes to 1  $\mu$ . The colpi are narrow, shallow and angular in their undulations. Lateral branching is sporadic. When present, the branches are long and widely spaced, occurring every 6–7  $\mu$ ; secondary branching is absent. At the equator the ridges average 10  $\mu$  in width at the base and 1.4–1.8  $\mu$  at the crest. In optical section the ectexine along the ridge crest is verrucate with the verrucae low and semicircular in outline. They average 3.5–5  $\mu$  in length.

### *Ephedra funera* Cov. & Mort.

PLATE II, fig. 5.

Polar axis 69  $\mu$  (43–81.8  $\mu$ ); equatorial diameter 40  $\mu$  (36–45  $\mu$ ). Ridges 8.3 (6–13). Shape class index 1.7 (1.5–1.9); prolate.

This species differs from the preceding in possessing pollen of larger size with smooth, non-verrucate ridges. However, in optical section the ridge crest may appear slightly irregular in outline. At the equator the ridges measure 8–10  $\mu$  in width at the base and 2.4–2.8  $\mu$  in width at the crest.



Although the colpi are straight, occasional angular undulations may occur. There is no evidence of lateral branching.

Thickness of ectexine at the ridge crest at the equator  $2-3\ \mu$ , at the poles  $1.5\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of endexine  $1.4\ \mu$ .

### *Ephedra gerardiana* Wall.

Polar axis  $52\ \mu$  ( $35-63\ \mu$ ); equatorial diameter  $25\ \mu$  ( $21-27\ \mu$ ). Ridges  $9.0$  ( $8-11$ ). Shape class index  $2.0$  ( $1.5-2.6$ ); prolate-perprolate.

The grains are characterized by straight, wide-crested ridges which are slightly irregular in texture. In polar view they are triangular in shape, extending  $2-3\ \mu$  in height, and measuring  $5-8\ \mu$  in width along the base and  $1.5\ \mu$  at the crest. The ridges may undulate at the equator, the undulations ceasing near the poles. The colpi may be straight or very slightly undulant with the undulations angular and set close together. Lateral branching may or may not occur. When it does occur the branches are extremely short and shallow; consequently the furrow area is psilate, although there is a slight evidence of verrucate sculpturing along the ridge crest.

Thickness of ectexine at the ridge crest at the equator  $2-3\ \mu$ , at the poles  $1.5\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of endexine  $0.8\ \mu$ .

### *Ephedra graeca* C. A. Mey.

Polar axis  $62\ \mu$  ( $49-72\ \mu$ ); equatorial diameter  $31\ \mu$  ( $25.5-34.5\ \mu$ ). Ridges  $6.5$  ( $5-9$ ). Shape class index  $1.8$  ( $1.6-2.6$ ); prolate.

The exine is thicker than in *Ephedra distachya*, measuring  $5\ \mu$  at the ridge axis at the equator and  $2-3\ \mu$  at the poles. It decreases in thickness to  $0.7-1\ \mu$  in the furrow region and appears to be absent over the colpi. The endexine is continuous and averages  $0.8-1.5\ \mu$  in thickness. The colpi are narrow, averaging  $0.8\ \mu$  in width, angular and undulate to the poles, branching every  $5-7\ \mu$ . Secondary branching is lacking but the sides of the ridge are highly dissected by long, primary, lateral colpi. The verrucae along the ridge crest are not as prominent as in *E. coryi* nor as numerous as in *E. distachya*. In optical section their surface appears flat or only slightly rounded. They vary in length from  $5$  to  $7\ \mu$ . The average width of the ridges at the equator varies from  $10\ \mu$  at the base to  $3.5\ \mu$  at the crest.

### *Ephedra helvetica* C. A. Mey.

Polar axis  $57\ \mu$  ( $43-67\ \mu$ ); equatorial diameter  $27\ \mu$  ( $21-33\ \mu$ ). Ridges  $6.9$  ( $5-9$ ). Shape class index  $2.0$  ( $1.6-2.5$ ); prolate-perprolate.

The grains are coarser in appearance than those of *Ephedra distachya* and are so similar in structure to *E. graeca* that pollen of these species cannot be distinguished. The ectexine averages  $4-5\ \mu$  in thickness at the ridge crest at the equator and  $2\ \mu$  at the poles. It decreases to  $1\ \mu$  in the furrow region. The endexine measures  $1-1.5\ \mu$ . Individual verrucae average  $7-8\ \mu$  in length.

***Ephedra intermedia* Schrenk & C. A. Mey.**

Polar axis  $54\ \mu$  ( $34\text{--}65\ \mu$ ); equatorial diameter  $25.5\ \mu$  ( $20\text{--}31\ \mu$ ). Ridges  $7.8$  ( $6\text{--}10$ ). Shape class index  $1.9$  ( $1.2\text{--}2.2$ ); prolate-perprolate.

Although the verrucate ridge is composed of series of smaller, angular verrucae, set close together, measuring  $2\text{--}3\ \mu$  in length, the grains appear coarser than those of *E. distachya* as a result of the thicker exine. At the equator the ridges average  $6\text{--}7\ \mu$  in width at the ridge base and  $3.5\text{--}4\ \mu$  at the apex; the width of the furrow area ranges between  $5\text{--}5.5\ \mu$ . In optical section the ridge surface appears almost smooth because of the shallowness of the dissecting grooves. The colpi are thin, shallow and slightly angular in their undulation. Secondary branching does not occur.

Thickness of the ectexine at the ridge crest at the equator  $4\text{--}5\ \mu$ , at the poles  $2\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of the endexine  $1.5\text{--}1.8\ \mu$ .

***Ephedra major* Host var. *procera* Aschers. & Graebn.**

Polar axis  $56\ \mu$  ( $37\text{--}68\ \mu$ ); equatorial diameter  $23\ \mu$  ( $20\text{--}27\ \mu$ ). Ridges  $6.3$  ( $5\text{--}8$ ). Shape class index  $2.3$  ( $1.9\text{--}2.6$ ); prolate-perprolate.

The ridge surface is verrucate. In optical section the verrucae are distinctly visible, slightly rounded and average  $5\text{--}6\ \mu$  in length. At the equator the ridges average  $8\text{--}10\ \mu$  in width at the base and  $3\ \mu$  in width at the crest. The furrow region measures  $5\text{--}8\ \mu$  in width. The colpi are thin, averaging  $0.5\ \mu$  in width, extremely faint and slightly rounded in their undulations. Long, primary branches of the main colpi occur every  $2\text{--}6\ \mu$ .

Thickness of the ectexine at the ridge crest at the equator  $4\ \mu$ , at the poles  $2\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of the endexine  $0.5\text{--}0.8\ \mu$ .

***Ephedra major* Host var. *villarsii* Stapf**

Polar axis  $59\ \mu$  ( $33\text{--}74\ \mu$ ); equatorial diameter  $27\ \mu$  ( $20\text{--}33\ \mu$ ). Ridges  $6.5$  ( $5\text{--}8$ ). Shape class index  $1.9$  ( $1.6\text{--}2.6$ ); prolate.

These grains are similar to those of *E. equisetina* and *E. monostachya* in the possession of a characteristically thin exine which is composed of an ectexine measuring  $0.8\text{--}1.4\ \mu$  in thickness along the ridge crest and an endexine averaging  $0.5\text{--}0.8\ \mu$ . The thickness of the ectexine in the furrow region decreases to  $0.5\text{--}0.8\ \mu$ . The colpi are narrow and shallow measuring  $0.5\ \mu$  in depth, and slightly undulate to the poles. Sporadic lateral branching may occur. In some cases these may be cut off every  $5.5\text{--}7\ \mu$  along the course of the main colpi. However, they seldom continue up the ridge surface to its crest. The delicacy of the grain is due to the absence of reticulation or to the extremely faint reticulation on the ridges. The ridges are slightly verrucate along the crest, with verrucae semicircular in outline. These average  $2.8\text{--}3.5\ \mu$  in length and are low, ranging in height from  $0.8$  to  $1\ \mu$ . At the equator the width of the ridges at the base is  $9\ \mu$  and at the crest is  $1\ \mu$ .

***Ephedra monostachya* L.**

Polar axis  $56\ \mu$  ( $42\text{--}75\ \mu$ ); equatorial diameter  $32\ \mu$  ( $22\text{--}39\ \mu$ ). Ridges  $7.3$  ( $6\text{--}9$ ). Shape class index  $1.6$  ( $1.3\text{--}1.8$ ); prolate.

As in the case of *E. equisetina*, the grains are characterized by thin exines, with ectexines measuring  $1.5\text{--}2\ \mu$  along the ridge crest and endexines measuring  $0.5\text{--}0.8\ \mu$  in thickness. The ridges are delicate, and irregularly verrucate with the length of the individual verrucae varying from  $4\text{--}8\ \mu$ . In optical section the verrucae average  $1\text{--}1.4\ \mu$  in height along the ridge crest and the majority are gently domed along their protruding surface. Colpi are shallow, averaging  $0.8\ \mu$  in depth, and slightly undulate with only occasional branching.

### *Ephedra pachyclada* Boiss.

Polar axis  $55\ \mu$  ( $43\text{--}68\ \mu$ ); equatorial diameter  $30\ \mu$  ( $27\text{--}36\ \mu$ ). Ridges  $7.9$  ( $5\text{--}12$ ). Shape class index  $1.7$  ( $1.1\text{--}1.9$ ); prolate.

The grain is featured by an endexine which may be as thick as the ectexine. The colpi are narrow, shallow and acutely angular in surface view. Short, lateral branches occur every  $2\text{--}3\ \mu$  at the apices of the angles. Secondary branching seldom occurs. As a result of the shallowness of the lateral branches of the colpus the verrucae are indistinct. They average  $2\text{--}3\ \mu$  in length. In optical section their surfaces are slightly rounded. At the equator the ridges average  $5.5\text{--}8\ \mu$  in width at the base and  $3\ \mu$  in width at the crest.

Thickness of the ectexine at the ridge crest at the equator  $2\text{--}3\ \mu$ , at the poles  $1.5\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of the endexine  $1.6\text{--}2\ \mu$ .

### *Ephedra sinica* Stapf    PLATE I, fig. 2; PLATE III, figs. 3-6; PLATE IV, figs. 5, 6.

Polar axis  $54\ \mu$  ( $42\text{--}62\ \mu$ ); equatorial diameter  $28\ \mu$  ( $25\text{--}31\ \mu$ ). Ridges  $5.8$  ( $4\text{--}6$ ). Shape class index  $1.6$  ( $1.4\text{--}1.8$ ); prolate.

This species possesses the most highly ornamented pollen grains to be found in the genus. They are sculptured by four to six steep, undulating ridges which project sharply above the rounded contours of the grain. The ridge undulations are slightly rounded to angular and the wave of the undulation measures between  $3$  and  $5\ \mu$  in length and  $3$  and  $4\ \mu$  in height. Furthermore, small ectexinous ridges, or muri,  $0.8\text{--}1\ \mu$  wide, extend out from the crest of the ridge into the inter-ridge area in a rugulate-reticulate sculpturing pattern enclosing lumina  $2\text{--}4\ \mu$  in diameter.

Viewed in the equatorial plane, the grain is prolate to ellipsoidal, whereas in polar aspect the outline is polygonal with the ridges situated at the angles of bulging, convex sides. Also in polar view, it may be seen that the ridges are rounded, with an average diameter of  $1.5\ \mu$ , a height of  $4\text{--}5\ \mu$  and are slightly constricted at their bases.

Occasionally, evidence of a thin, slightly branched colpus at the base of the ridge can be seen. However, when present the colpus is indistinct.

The exine is double. The ectexine, at the center of the ridge at the equator varies from  $4$  to  $5\ \mu$  in thickness, decreasing slightly toward the poles. In polar view, the ectexine abruptly thins, at the base of the ridge, ceasing altogether at the colpi. The endexine is  $2\text{--}3\ \mu$  thick. In profile



view, the ectexine appears to be composed of baculae  $4\ \mu$  high and  $2\ \mu$  wide. These are merely the optical sections of the undulating ridge.

### *Ephedra viridis* Cov.

PLATE IV, *figs. 1, 2.*

Polar axis  $61\ \mu$  ( $44\text{--}77\ \mu$ ); equatorial diameter  $34\ \mu$  ( $30\text{--}39\ \mu$ ). Ridges 7.1 (5–9). Shape class index 1.7 (1.5–1.9); prolate.

The grains are characterized by straight, thin-crested, smooth ridges. The main, longitudinal colpi are distinct, narrow and acutely angular. Short lateral branches occur every  $2\text{--}3\ \mu$  and an occasional secondary branch may be found. In optical section, verrucae are evident but they are faint because of the shallowness of the lateral colpi and their surface outline is flattened. At the equator the ridges average  $10\text{--}14\ \mu$  in width at the base and  $3.5\ \mu$  at the crest.

Thickness of the ectexine at the ridge crest at the equator  $3\ \mu$ , at the poles  $2\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of the endexine  $1.5\ \mu$ .

### *Ephedra vulgaris* C. A. Mey.

Polar axis  $51\ \mu$  ( $49\text{--}57\ \mu$ ); equatorial diameter  $28\ \mu$  ( $25\text{--}31\ \mu$ ). Ridges 7. Shape class index 1.7 (1.5–1.9); prolate.

The ridges are smooth, measuring at the equator  $3\ \mu$  in width at the crest and  $7\text{--}10\ \mu$  at the base. The colpi are thin grooves which branch occasionally but, as in the case of *Ephedra funera*, the lateral branches do not continue far up the ridge.

Thickness of the ectexine at the ridge crest at the equator  $2\text{--}3\ \mu$ , at the poles  $0.7\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of the endexine  $1\ \mu$ .

## POLLEN TYPE B

This type is approximately of the same size as Type A. The majority of grains are basically polycolpate, although the colpus is often indistinct, and all are sculptured by ectexinous ridges extending meridionally across the grain merging with those from the opposite side.

However, the grains differ significantly from the preceding type in furrow and ridge characteristics. In Type B the ectexine is thickened irregularly to form extremely narrow, undulating, psilate ridges. When viewed in the equatorial plane the narrow ridges appear as highly refractive, smooth, serpentine lines extending the length of the grain. In some cases as in *Ephedra californica*, the undulations continue to the poles; in others, as *E. altissima*, the height of the ridge as well as the degree of undulation decreases at the poles.

The number of ridges in Type B is generally more numerous than in Type A, ranging, on the average, from 10 to 13. The least amount of variation in our material occurs in *E. californica* where the number of ridges ranges from 10 to 14; the greatest amount of variability was observed in *E. pedunculata* where the ridge number ranges from 9 to 17 (CHART II). The high degree of variability within some species results

CHART II

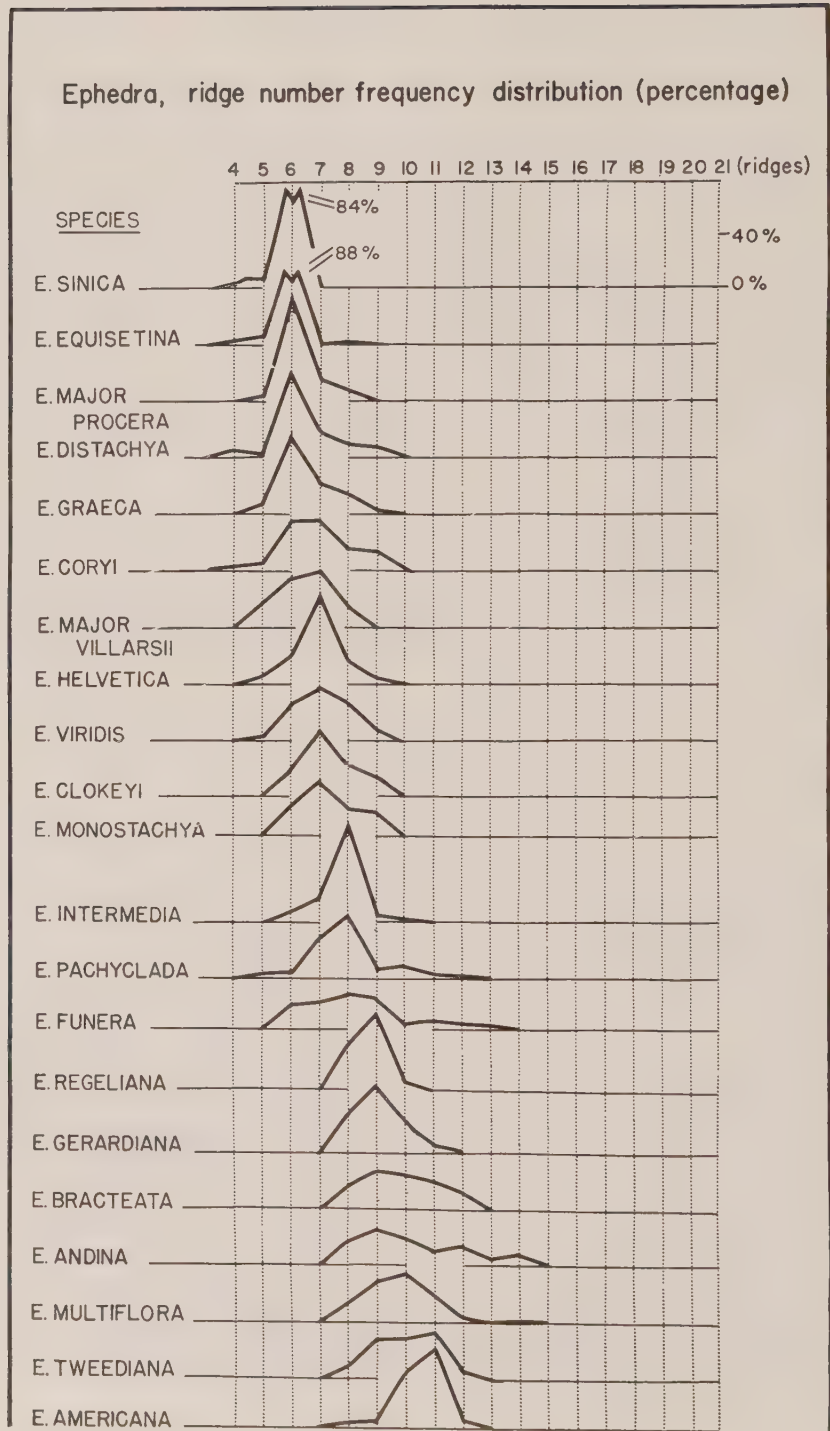
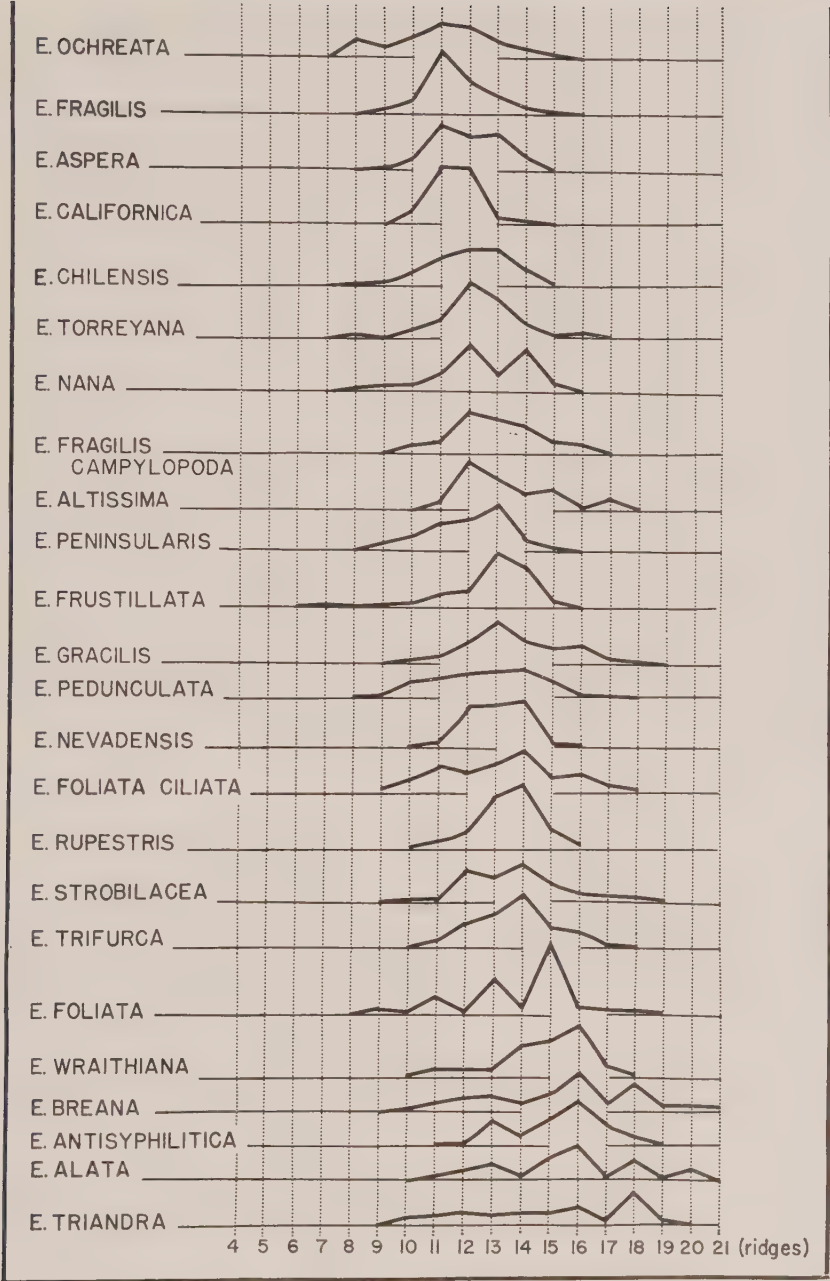


CHART II (Continued)





in a few individual cases of overlapping values with respect to ridge number in Types A and B. This somewhat lessens the value of but does not preclude the use of this characteristic, in conjunction with others, as a means of separating the two groups. The high amount of intraspecific variation does, however, prevent the use of this characteristic alone in separating species within each group, or in distinguishing between groups.

The exine is distinctly double and is composed of a thin, continuous endexine and an ectexine which may be continuous or discontinuous. The ectexine is laid down in the form of ridges which in polar view are triangular in outline. In this aspect the highly refractive component of the ridge comprises the central core of the triangle which, according to Welton (1957), varies in shape depending upon species. This, in turn, is covered by the non-hyaline layer. Both of these different layers form the ectexinous ridge. In this respect the structure of the ridge is similar to that found in Type A as well as in Type C. The width of the base of the triangle may vary from 2 to 4  $\mu$ , decreasing at the top to a narrow peak of 0.5 to 1  $\mu$ ; the height of the ridge may range from 2 to 3.5  $\mu$ . The ridges are not as massive as in the Type A group. Consequently, the grains appear more delicate, an appearance enhanced by the lack of verrucae along the ridge and the absence of reticulate sculpturing in the furrows.

In a few species colpi are absent.<sup>5</sup> When colpi are present they are located at the base of the furrow, extending unbranched their full length. Moreover, the distinctness of the colpi varies between species, depending upon whether the colpus is the result of a complete absence or merely a thinning of the ectexine. In *E. chilensis* the colpi are only occasionally discernible, whereas in *E. tweediana* well defined colpi can be observed.

#### DESCRIPTIONS OF SPECIES OF TYPE B

##### *Ephedra altissima* Desf.

Polar axis 40  $\mu$  (30–49  $\mu$ ); equatorial diameter 23  $\mu$  (21–27  $\mu$ ). Ridges 13.3 (11–17). Shape class index 1.6 (1.4–1.8); prolate.

The ridges undulate slightly in the equatorial region of the grain, gradually ceasing near the poles. In polar view the ridges measure 5–6  $\mu$  in width at the base and decrease to a peak 1–1.5  $\mu$  wide. The thickness or height of the ectexinous ridges averages 2–3  $\mu$  at the equator. The ridge undulations are variable in extent and may average 4–8  $\mu$  in length and 2–3  $\mu$  in width. A faint, unbranched, straight colpus is present at the base of each ridge.

Thickness of the ectexine in the furrow region 0.8  $\mu$ ; thickness of the endexine 1  $\mu$ . At the poles the ectexine often projects 5–6  $\mu$  beyond the endexine.

##### *Ephedra antisiphilitica* Berland.

Polar axis 59  $\mu$  (42–59  $\mu$ ); equatorial diameter 43  $\mu$  (33–49  $\mu$ ). Ridges 15.3 (12–18). Shape class index 1.4 (1.2–1.8); prolate.

<sup>5</sup> For our definition of colpus as applied to *Ephedra* pollen see footnote 4.

This species possesses the largest pollen grains in the group. These may be further characterized by the presence of an extremely tenuous ectexine which easily becomes dissociated from the endexine. The ectexine may become free at one pole only, at both poles, or irregularly around the entire grain. The ectexine is irregularly thickened forming ridges which measure  $2.5\ \mu$  in height at the equator. In the polar aspect they are triangular in shape and at the equator average  $2.5\text{--}5\ \mu$  in width at the base and  $0.7\ \mu$  at the crest. The ridges may be either highly undulate, slightly undulate or, in a few cases, almost straight. A slightly undulate, faint, unbranched colpus is present between each ridge. The thickness of the ectexine decreases to  $0.5\ \mu$  in the furrow region. The endexine averages  $1\ \mu$  in thickness.

***Ephedra californica* S. Wats.** PLATE I, fig. 5; PLATE III, figs. 1, 2.

Polar axis  $63\ \mu$  ( $53\text{--}77\ \mu$ ); equatorial diameter  $32\ \mu$  ( $21\text{--}40\ \mu$ ). Ridges  $11.5$  ( $10\text{--}14$ ). Shape class index  $2.0$  ( $1.5\text{--}2.5$ ); prolate-perprolate.

The grains are characterized by ridges  $6\text{--}7\ \mu$  apart that zigzag meridionally the length of the grain. In polar view, the ridges appear triangular with a base measuring  $3\text{--}4\ \mu$  in width, decreasing to a thin crest of  $0.5\text{--}1\ \mu$ . The serpentine ridge undulates sharply throughout its length. The ectexine is  $2.4\text{--}3.2\ \mu$  thick at maximum at the equator, decreasing to  $0.5\text{--}1\ \mu$  in the furrows. The endexine measures  $1\text{--}1.6\ \mu$ . Slightly undulant colpi may be present. The type of undulation varies from tightly angular to widely spaced and semicircular. Occasional primary branches of the main colpi are evident.

***Ephedra chilensis* Miers**

PLATE IV, fig. 3.

Polar axis  $52\ \mu$  ( $35\text{--}68\ \mu$ ); equatorial diameter  $30\ \mu$  ( $27\text{--}31\ \mu$ ). Ridges  $11.9$  ( $8\text{--}14$ ). Shape class index:  $1.6$  ( $1.3\text{--}1.8$ ); prolate.

Among the Type B species, these grains are distinctive in the greater thickness of their exine. The ectexine averages  $2\text{--}3\ \mu$  along the ridge crest; the endexine measures  $1.5\text{--}2.8\ \mu$ . A thin, serpentine, straight colpus may be visible in each furrow. The ridges are undulant to a varying degree. At the equator they average  $5\text{--}6\ \mu$  in width at the base and  $0.5\ \mu$  at the crest.

Thickness of the ectexine at the furrow region  $1\text{--}1.4\ \mu$ . As in some of the preceding grains, the ectexine at the poles may project as much as  $5\ \mu$  beyond the endexine.

***Ephedra fragilis* Desf. var. *campylopoda* (C. A. Mey.) Stapf**

Polar axis  $56\ \mu$  ( $44\text{--}66\ \mu$ ); equatorial diameter  $30\ \mu$  ( $22.5\text{--}36\ \mu$ ). Ridges  $12.9$  ( $10\text{--}16$ ). Shape class index  $1.8$  ( $1.2\text{--}2.4$ ); prolate-perprolate.

Although larger than most members of this group, the pollen grains of this species are smaller than those of *Ephedra californica* or *E. antisiphilitica*. The ridges are narrow at the crest, varying from  $1\text{--}1.5\ \mu$ ; wide at the base, the width averaging  $2\text{--}3\ \mu$ ; and measure  $0.8\text{--}1\ \mu$  in height at the equator. The ridge crest is acutely undulate with undulations averaging

2.5–5  $\mu$  in length and 2.5  $\mu$  in width. However, the degree of undulation tends to diminish toward the poles. Indistinct, thread-like, straight colpi are present.

There is a strong tendency for the endexine and the ectexine to separate resulting in the shedding of the ectexine by the grain. This separation is evident at the poles where the ectexine becomes detached and projects out 3–5  $\mu$  beyond the endexine to form rectangular enclosures between the two exine layers.

Thickness of the ectexine at the ridge crest at the poles 0.5  $\mu$ , in the furrow region 0.5  $\mu$ ; thickness of the endexine 0.5  $\mu$ .

### *Ephedra multiflora* Phil. ex Stapf

Polar axis 41.5  $\mu$  (31.5–51  $\mu$ ); equatorial diameter 24  $\mu$  (20–30  $\mu$ ). Ridges 9.8 (8–14). Shape class index: 1.6 (1.1–2.0); prolate.

The grains are similar to those of *Ephedra tweediana* in their small size, and resemble *E. fragilis* var. *campylopoda* in a tendency to shed their ectexine. The ectexine is 2–3  $\mu$  thick at the ridge crest at the equator, often ballooning out 5–6  $\mu$  beyond the endexine at the poles. The ridges are featured by a few minor undulations measuring 6–7  $\mu$  in length and 3–3.5  $\mu$  in width. At the equator the ridges average 7  $\mu$  in width at the base and less than 1  $\mu$  at the crest. Distinct but thin, straight, unbranched colpi are present.

Thickness of the ectexine in the furrow region 0.8  $\mu$ ; thickness of the endexine 0.8–1.2  $\mu$ .

### *Ephedra nevadensis* S. Wats.

PLATE IV, fig. 7.

Polar axis 35  $\mu$  (31.5–45  $\mu$ ); equatorial diameter 22  $\mu$  (18–27  $\mu$ ). Ridges 13.0 (11–15). Shape class index 1.6 (1.4–1.9); prolate.

Characteristic features of these grains are the closely undulate colpi which extend along the center of the furrows. The undulations are angular and occur every 2–2.5  $\mu$ .

The ridge crests are extremely thin and vary from straight to closely undulate with waves which range in length from 2–2.5  $\mu$  and in width from 1.4–1.8  $\mu$ . At the equator the ridges measure 3.5–5  $\mu$  in width at the base and 0.3–0.5  $\mu$  at the crest.

Thickness of the ectexine at the ridge crest at the equator 2.8  $\mu$ , at the poles 1.5  $\mu$ ; thickness of the endexine 0.8  $\mu$ . The ridges project out a distance of 2.8  $\mu$  beyond the endexine at the poles.

### *Ephedra pedunculata* Engelm. ex S. Wats.

Polar axis 48  $\mu$  (40–60  $\mu$ ); equatorial diameter 29  $\mu$  (25–39  $\mu$ ). Ridges 12.6 (9–17). Shape class index 1.6 (1.4–1.8); prolate.

The ectexine is thicker than the endexine, measuring 2.8  $\mu$  at the ridge crest at the equator and 2  $\mu$  at the poles. In polar view the ridge measures 3.5–7  $\mu$  in width at the base, decreasing to 0.7–0.1  $\mu$  at the crest. The colpi are indistinct, thin and slightly undulate. Ridge undulations are irregular



in occurrence and measure 4–6  $\mu$  in length and 1.5–3.5  $\mu$  in width. The thickness of the endexine is 1.6  $\mu$  increasing to 2–2.5  $\mu$  at the poles.

***Ephedra tweediana* Fisch. & C. A. Mey.**

Polar axis 42  $\mu$  (21–55  $\mu$ ); equatorial diameter 25  $\mu$  (24–28  $\mu$ ). Ridges 10 (8–12). Shape class index 1.7 (1.4–1.9); prolate.

The grains of this species are ornate with highly undulant ridges. At the poles the fused ridges abruptly project forming a circular process at each end of the grain. The ridges are high, projecting 5  $\mu$  at the equator. Their basal width at the equator varies from 4 to 12  $\mu$ ; the crests average 0.5–1  $\mu$ . A distinct, straight colp is present.

Thickness of the ectexine in the furrow region 2  $\mu$ ; thickness of the endexine 1.5  $\mu$ .

### POLLEN TYPE C

Although similar to Type B in many respects, the ridge structure in Type C is prevailingly different. The ridges are somewhat higher than in Type B, and usually straight. In some cases, however, there is a tendency for slight undulation in the ridge crest. Although in their most characteristic form the two types are readily separable, there is a tendency in some species for pollen grains to exhibit features of both the B and C types. Hence the Type B and Type C categories are not consistently separable as other than varying degrees of morphological expression. It might be argued that the two types should be merged as one, but in our opinion there is a preponderance of one or the other within a given species, and hence the concept has morphological validity. As will be shown later there is no difficulty in distinguishing the A types from the D types, nor is there in distinguishing the C from the D nor the A from the C types. In this respect we are dealing with a continuous spectrum of structural variation on which arbitrary limits are imposed.

### DESCRIPTIONS OF SPECIES OF TYPE C

***Ephedra americana* Humb. & Bonpl. ex Willd.** PLATE II, *figs. 6, 7.*

Polar axis 38  $\mu$  (27–49  $\mu$ ); equatorial diameter 25  $\mu$  (21–30  $\mu$ ). Ridges 10.5 (8–12). Shape class index 1.6 (1.2–1.8); prolate.

A conspicuous feature of these grains is the outbulging of the ectexine which may exceed 6  $\mu$  on one or both sides, or circumferentially around the complete grain freeing the two layers of the exine.

In those cases in which the ectexine is attached to the endexine, it measures 2–2.5  $\mu$  in thickness at the equator and slightly thicker (3  $\mu$ ) at the poles. The average thickness of the endexine is 2  $\mu$ . With separation of the exine layers the whole grain expands. However, the furrowed ectexine is more flexible than the continuous endexine and expands to a greater degree, resulting in an ectexine “shell” measuring approximately  $40 \times 30 \mu$  and an endexine “shell” whose average dimensions are  $30 \times 20 \mu$ .

This disproportionate increase in diameter of the two wall layers of the grain effects a decrease in thickness of the ektexine and endexine proportionately. The average thickness of the ektexine in the mature grain is from 1 to 1.2  $\mu$ ; whereas the thickness of the endexine remains slightly under 2  $\mu$ . Because of the variable nature of the ektexine, the outline of the grain in both polar and equatorial views is highly irregular, but the endexine appears regular in outline and prolate in shape. The ridge crests are narrow, averaging 1  $\mu$  in width at the equator and are spaced 4–5  $\mu$  apart. At the base of each furrow is a distinct, thread-like, unbranched colpus.

***Ephedra andina* Poepp. & Endl.**

PLATE IV, fig. 4.

Polar axis 53  $\mu$  (42–63  $\mu$ ); equatorial diameter 27  $\mu$  (24–30  $\mu$ ). Ridges 10.3 (8–14). Shape class index 1.8 (1.7–2.1); prolate.

These grains possess the characteristic, psilate ridges of Type C. At the equator they may measure as much as 4  $\mu$  in height. The base of the ridge averages 5  $\mu$  in width at the equator, and 0.5–0.8  $\mu$  at the crest. The majority of ridges are straight. A narrow, slightly undulating, unbranched colpus is visible at the base of each furrow. The ektexine is thicker than the endexine and averages 3  $\mu$  along the ridge crest, thinning to 1  $\mu$  in the furrow. The endexine averages between 2  $\mu$  and 2.5  $\mu$  in thickness. There is a slight projection of the ektexine at the poles.

***Ephedra aspera* Engelm. ex S. Wats.**

PLATE I, fig. 1; PLATE IV, fig. 8.

Polar axis 50  $\mu$  (42–59  $\mu$ ); equatorial diameter 25  $\mu$  (22–27  $\mu$ ). Ridges 11.9 (9–14). Shape class index 1.8 (1.5–2.2); prolate.

The ridges are thin and slight, rising 1.6–2.5  $\mu$  above the endexine at the equator, decreasing to 1  $\mu$  at the poles. At the equator they measure 4–5  $\mu$  in width at the base and 1  $\mu$  at the ridge crest. A conspicuous feature of the grains is the projection of the ektexine 3–4  $\mu$  beyond the endexine forming small, handle-like structures at both poles. A narrow, slightly undulating colpus is present at the base of each furrow.

Thickness of the ektexine in the furrow region 0.5  $\mu$ ; thickness of the endexine 1.6  $\mu$ .

***Ephedra bracteata* Miers**

Polar axis 50  $\mu$  (42–60  $\mu$ ); equatorial diameter 29  $\mu$  (25–33  $\mu$ ). Ridges 9.8 (8–12). Shape class index 1.6 (1.5–1.7); prolate.

In contrast to the thin, smooth condition of the ridges in *Ephedra aspera*, the ridges in *E. bracteata* are heavy, wide and slightly irregular in surface view. At the equator they measure 5–7  $\mu$  in width at the base and 2  $\mu$  in width at the ridge crest. The bases of the ridges are cut by an irregular, highly undulate colpus which occasionally branches.

Thickness of the ektexine at the ridge crest at the equator 3–3.5  $\mu$ , at the poles 2  $\mu$ , in the furrow region 1  $\mu$ ; thickness of the endexine 3  $\mu$ .

***Ephedra foliata* Boiss. & Kotschy ex. Boiss.**

Polar axis  $44\ \mu$  (30–53  $\mu$ ); equatorial diameter  $28\ \mu$  (22–30  $\mu$ ). Ridges 13.9 (9–18). Shape class index 1.6 (1.4–2.0); prolate.

The grains are featured by narrow, straight ridges, measuring 4–7  $\mu$  in width at the base at the equator and 0.5–1  $\mu$  at the crest. They extend 1.8–2.5  $\mu$  in height at the equator decreasing to 1.4  $\mu$  at the poles. The majority of the ridges are straight but a few undulating ones are present. A narrow, straight colpus is present at the base of each furrow.

Thickness of the ectexine in the furrow region 0.5  $\mu$ ; thickness of the endexine 2  $\mu$ .

***Ephedra foliata* Boiss. var. *ciliata* (C. A. Mey.) Stapf**

Polar axis  $47\ \mu$  (44–54  $\mu$ ); equatorial diameter  $29\ \mu$  (25–36  $\mu$ ). Ridges 13.2 (10–17). Shape class index 1.5 (1.1–1.7); prolate.

The ridges are narrow and straight, measuring 3.5  $\mu$  in height at the equator, decreasing to 2  $\mu$  at the poles. At the equator they average 3.5–4  $\mu$  in width at the base and 0.5  $\mu$  at the crest. Thin, thread-like colpi are present at the base of each furrow.

Thickness of the endexine 1.4  $\mu$ .

***Ephedra fragilis* Desf.**

Polar axis  $53\ \mu$  (44–63  $\mu$ ); equatorial diameter  $33\ \mu$  (28–51  $\mu$ ). Ridges 11.5 (9–15). Shape class index 1.5 (1.3–1.7); prolate.

The grain appears almost spherical in equatorial view with projecting, ectexinous ridges at the poles. The ridges measure 1–1.5  $\mu$  in height at the equator and project a distance of 3–4  $\mu$  beyond the polar limits of the endexine.

With high magnification, the crest of the ridges exhibits tight undulations; under low power there is little evidence of this condition and the ridge crests appear straight. The ridge crests are thin, averaging 0.5  $\mu$  at the equator; the bases of the ridges are wider, averaging 5  $\mu$  at the equator and decreasing to 1.4  $\mu$  at the poles. A thin but distinct, slightly undulating colpus is present in each furrow.

Thickness of the ectexine in the furrow region 0.8  $\mu$ ; thickness of the endexine 2  $\mu$ .

***Ephedra frustillata* Miers**

Polar axis  $48\ \mu$  (30–60  $\mu$ ); equatorial diameter  $30\ \mu$  (28–36  $\mu$ ). Ridges 12.7 (7–15). Shape class index 1.5 (1.2–1.7); prolate.

These differ from some of the preceding grains in the larger size and in the absence of any tendency toward separation of the exine layers. In company with *Ephedra regeliana* and *E. ochreatea* they possess a thin exine which measures 1.5  $\mu$  along the ridge crest at the equator, a thin endexine of 0.8  $\mu$ , and narrow, straight ridges.

Thickness of the ectexine at the ridge crest at the poles 1  $\mu$ , in the furrow region 0.5  $\mu$ .



***Ephedra nana* Dusen**

Polar axis  $46\ \mu$  ( $35\text{--}60\ \mu$ ); equatorial diameter  $27\ \mu$  ( $24\text{--}30\ \mu$ ). Ridges  $12.4$  ( $8\text{--}15$ ). Shape class index  $1.6$  ( $1.4\text{--}2.0$ ); prolate.

The grains possess ridges of the Type C structure which are bordered at their bases by thin, tightly undulate or straight colpi. The ridges average  $3.5\text{--}5\ \mu$  in width at the equator at the base and  $0.5\ \mu$  at the crest.

Thickness of the ectexine along the ridge crest at the equator  $2\ \mu$ , at the poles  $0.7\text{--}1\ \mu$ ; thickness of the endexine  $1.5\ \mu$ . The ectexine projects  $2.5\text{--}3\ \mu$  beyond the endexine at the poles.

***Ephedra ochreatea* Miers**

Polar axis  $41\ \mu$  ( $27\text{--}51\ \mu$ ); equatorial diameter  $22\ \mu$  ( $18\text{--}30\ \mu$ ). Ridges  $11.0$  ( $8\text{--}15$ ). Shape class index  $1.7$  ( $1.6\text{--}2.0$ ); prolate.

The exine is thin, the ectexine measuring  $0.8\text{--}1.4\ \mu$  in thickness along the ridge crest; the endexine as thick as the ectexine or slightly more so varying between  $1$  and  $1.5\ \mu$ . In the furrow region the thickness of the ectexine decreases to  $0.5\ \mu$ . A slight increase in thickness of the ectexine may or may not occur at the poles. At the equator the width of the ridges at the base averages  $3.5\text{--}6\ \mu$ ; that of the ridge crest is  $0.7\ \mu$ . A tightly undulate to straight colpus is present at the base of each ridge. In optical section the ridge crest is minutely irregular in outline.

Sculpturing of the ectexine: slightly scabrate.

***Ephedra peninsularis* I. M. Johnston**

Polar axis  $52\ \mu$  ( $38\text{--}63\ \mu$ ); equatorial diameter  $30\ \mu$  ( $30\text{--}31\ \mu$ ). Ridges  $11.9$  ( $9\text{--}15$ ). Shape class index  $1.6$  ( $1.5\text{--}1.8$ ); prolate.

The ridges are completely straight, averaging at the equator  $5\text{--}8.5\ \mu$  in width at the base and  $1\text{--}2\ \mu$  at the crest. Each furrow contains a distinct, thin, straight colpus. Although the surface of the ridge is psilate, the overall appearance of the grain is one of massiveness as a result of the thick exine.

Thickness of the ectexine at the ridge crest at the equator  $3\text{--}4\ \mu$ , at the poles  $4\ \mu$ , in the furrow region  $1\ \mu$ ; thickness of the endexine  $1.6\ \mu$ .

***Ephedra regeliana* Florin**

Polar axis  $38\ \mu$  ( $28\text{--}51\ \mu$ ); equatorial diameter  $19\ \mu$  ( $16\text{--}21\ \mu$ ). Ridges  $8.7$  ( $8\text{--}10$ ). Shape class index  $1.9$  ( $1.6\text{--}2.0$ ); prolate.

Distinctive because of size, this species, together with *E. americana*, possesses the smallest pollen grains of the group. However, the grains differ from those of *E. americana* in the possession of an ectexine which adheres closely to the endexine. The ridges are straight to slightly undulate, and measure  $1\text{--}2\ \mu$  in height at the equator decreasing to  $0.5\text{--}1\ \mu$  at the poles. At the equator they average  $5\text{--}7\ \mu$  in width at the base and  $1\text{--}1.2\ \mu$  at the crest. A slightly undulate colpus is present in each furrow.

Thickness of the ectexine in the furrow region  $0.5\ \mu$ ; thickness of the endexine  $0.5\ \mu$ .

***Ephedra torreyana* S. Wats.**

Polar axis  $51\ \mu$  (38–61  $\mu$ ); equatorial diameter  $27\ \mu$  (25–30  $\mu$ ). Ridges 12.3 (8–16). Shape class index 1.8 (1.5–2.0); prolate.

The exine is thin, composed of an ectexine measuring  $1.6\ \mu$  in thickness along the ridge crest, and an endexine equally as thick as the ectexine,  $1.6\ \mu$ . There is some tendency for the ectexine to project 2–3  $\mu$  beyond the polar limits of the grain. The ridges are straight and at the equator measure  $0.8\ \mu$  in width at the crest and  $4\ \mu$  through the base. Thin, unbranched straight or slightly undulant colpi are visible.

***Ephedra wraithiana* I. M. Johnston**

Polar axis  $50\ \mu$  (38–65  $\mu$ ); equatorial diameter  $26\ \mu$  (24–28  $\mu$ ). Ridges 14.8 (11–17). Shape class index 1.6 (1.4–2.1); prolate.

The grains are similar in structure to the preceding species. They possess characteristic Type C ridges measuring  $4.5$ – $5\ \mu$  in width at the base at the equator, and  $1\ \mu$  at the crest. Each furrow is featured by a thin, straight colpus. In optical section the ridges appear slightly irregular in outline.

**POLLEN TYPE D**

The grains of Type D are characterized by wide, low, gently rounded, ectexinous ridges which measure 2–3  $\mu$  in height and 3.5–9  $\mu$  in width. In polar view the ridges appear semicircular in outline, in contrast to the triangular outline of the ridges in the three preceding groups. The furrows which abruptly flank the ridges at their bases are narrow (1–3.5  $\mu$ ), unbranched and straight. They are the result of extreme thinning of the ectexine. No colpi are present.

Within this group occurs the species which possesses the greatest number of ridges, *E. alata* (CHART II). Moreover, the average number for the group as a whole is greater than in Types B and C. Pollen grains of the D type are quite distinctive and readily separable from the other pollen types. However, within some species, possessing predominantly Type D grains, occasional grains of the B and C types occur. None of the seven species possessing D type grains shows the least tendency toward the A type.

**DESCRIPTION OF SPECIES OF TYPE D*****Ephedra alata* Dcne.**

Polar axis  $57\ \mu$  (42–70  $\mu$ ); equatorial diameter  $35\ \mu$  (30–39  $\mu$ ). Ridges 15.6 (11–20). Shape class index 1.6 (1.4–1.8); prolate.

These grains are characterized by large size as well as by a granulate texture of the ectexine ridges. The ridges are sculptured by minute granules approximately  $0.5\ \mu$  in diameter scattered irregularly over the surface. They may be found in distinct clumps or widely separated. When the granules are widely spaced, there is some indication that the intervening

space is slightly pitted. The width of the ridges at the base varies from 4–7  $\mu$  at the equator to 2–3.5  $\mu$  at the poles, while the furrows measure 1–2  $\mu$  in width continuously along their complete length to their abrupt termination near the poles. The furrows are somewhat irregular in shape, and in surface view the ectexine of the furrow appears slightly granulate. The degree of sculpturing in the floor of the furrows is much less than on the ridges; the granules are smaller and less numerous.

In most cases the endexine is thicker than the ectexine, and may measure as much as 2.5  $\mu$  in thickness. The ectexine measures 1–1.5  $\mu$  at the center of the ridges at the equator but may project as much as 4  $\mu$  beyond the polar limits of the grain.

### *Ephedra breana* Phil.

PLATE IV, fig. 9.

Polar axis: 44  $\mu$  (34–54  $\mu$ ); equatorial diameter 32  $\mu$  (27–39  $\mu$ ). Ridges: 15.2 (10–16). Shape class index 1.3 (1.1–1.6); prolate.

Similar to *Ephedra rupestris*, these pollen grains are small and very compact in appearance. There is no tendency for the ectexine to project at the poles, although the ectexine is a little thicker there than at the equator. The average width of the ridges at their base at the equator varies between 3.5  $\mu$  and 4.5  $\mu$ .

Thickness of the ectexine at the ridge crest at the equator 2–3  $\mu$ , at the poles 4  $\mu$ , in the furrow region 1  $\mu$ ; thickness of the endexine 0.8–1.4  $\mu$ .

### *Ephedra gracilis* Phil.

Polar axis 56  $\mu$  (35–65  $\mu$ ); equatorial diameter 26  $\mu$  (24–31  $\mu$ ). Ridges 13.5 (10–18). Shape class index 1.9 (1.7–2.3); prolate.

The grains possess an average of 13 low ridges which measure 4–7  $\mu$  in width at the equator decreasing to 2.5–3  $\mu$  at the poles. The furrows are narrow, 1–1.5  $\mu$ , and slightly irregular in outline. The exine is composed of a variably thickened ectexine which averages 3–3.5  $\mu$  in thickness, the height of the ridges at the equator, decreasing laterally to 1  $\mu$  at the furrow, and a continuous endexine which measures 1.5–2  $\mu$  in thickness. The ectexine does not project at the poles.

### *Ephedra rupestris* Benth.

Polar axis 39  $\mu$  (37–45  $\mu$ ); equatorial diameter 28  $\mu$  (27–31  $\mu$ ). Ridges 13.5 (11–15). Shape class index 1.4 (1.2–1.6); prolate.

These grains are among the smallest of the type D group. The ectexine measures 2  $\mu$  at the central point of the ridge at the equator, but gradually thins laterally in the furrow, and increases poleward to 3.2  $\mu$ . The endexine measures 0.8–1.5  $\mu$  in thickness. The ectexine adheres closely to the endexine of the grain at the poles and there seems to be no tendency for separation. The basal width of the slightly rounded ridges at the equator is 8–9  $\mu$  decreasing to 6–7  $\mu$  at the poles. The ridges are separated by extremely straight, narrow, psilate furrows.



***Ephedra strobilacea* Bunge**

Polar axis  $44\ \mu$  ( $31\text{--}60\ \mu$ ); equatorial diameter  $26\ \mu$  ( $20\text{--}31\ \mu$ ). Ridges  $13.7$  ( $10\text{--}18$ ). Shape class index  $1.6$  ( $1.5\text{--}1.7$ ); prolate.

The ridges are thin, averaging  $3\ \mu$  at the equator. The thickness of the ectexine at the equator varies from  $0.8\ \mu$  in the furrow region to  $1.5\text{--}3\ \mu$  at the ridge crest. The endexine varies in thickness from  $1\text{--}1.5\ \mu$ . The ectexine projects  $4\text{--}4.5\ \mu$  beyond the endexine at the poles in a manner similar to the preceding species. An indistinct, threadlike, straight furrow is present.

***Ephedra triandra* Tul.**

Polar axis  $41\ \mu$  ( $32\text{--}49\ \mu$ ); equatorial diameter  $26\ \mu$  ( $24\text{--}28\ \mu$ ). Ridges  $15.0$  ( $10\text{--}19$ ). Shape class index  $1.4$  ( $1.3\text{--}1.7$ ); prolate.

The pollen grains closely resemble those of *Ephedra rupestris*. The ridges are low, measuring  $1.5\ \mu$  in height and  $4\text{--}5\ \mu$  in width at the equator.

Thickness of the ectexine at the ridge crest at the equator  $1.5\ \mu$ , at the poles  $1.5\ \mu$ , in the furrow region  $0.5\ \mu$ ; thickness of the endexine  $1.5\ \mu$ . The ectexine projects  $4\ \mu$  beyond the polar limits of the endexine.

***Ephedra trifurca* Torr.**

PLATE I, fig. 4; PLATE II, figs. 3, 4.

Polar axis  $53\ \mu$  ( $39\text{--}63\ \mu$ ); equatorial diameter  $29\ \mu$  ( $28\text{--}30\ \mu$ ). Ridges  $13.7$  ( $11\text{--}17$ ). Shape class index  $1.8$  ( $1.5\text{--}2.1$ ); prolate.

These grains possess the thinnest exine in the D type group. The thickness of the two exine layers at the equator averages between  $1.8$  and  $2.4\ \mu$ , of which  $0.8\text{--}1\ \mu$  is the thickness of the ectexine and  $1\text{--}1.4\ \mu$  is the thickness of the endexine. However, the thickness of the ectexine increases to  $2\ \mu$  at the poles. In addition, the ectexine ridges, after following the contour of the grain up to this point, project outward. As is characteristic of the Type D group the grains possess gently rounded, wide ridges  $2.8\text{--}5\ \mu$  in width. These narrow to  $2\text{--}3\ \mu$  at the poles. The ridges are separated by distinct, unbranched furrows which are slightly irregular in outline where they border the steep-sided ridges.

## DISCUSSION

The system of pollen classification presented here is based primarily on the number and structure of ectexine ridges, the size and form of the intervening furrows and the presence or absence and structure of the "colpi."<sup>6</sup> On the basis of these features, *Ephedra* grains may be divided into four groups, here designated as Types A, B, C and D. Pollen Types A and D represent the two extremes in the genus while Types B and C tend to be intermediate in ridge number and other characteristics. Furthermore, pollen grains of Type B seem to be more closely related to Type A (as is also true of Type C) than to Type D. Type A pollen grains tend to predominate

<sup>6</sup> For definition of our use of the term colpus see explanatory footnote 4.

in a taxonomically coherent group of species and there is less variation in ridge number within this group than in the other three. Furthermore, since the *average* ridge number in this group of species does not overlap with the *average* ridge number in other groups, species possessing grains of Type A may often be determined on the basis of ridge number alone. This is not the case for species possessing the other types of pollen because of the extensive variation within each group of species and even within a single species. The three remaining groups of species are separated by the use of other characters of the ridges, such as height, steepness of slope and shape in polar view. To a considerable extent this classification system possesses practical value only in separating species featured predominantly by the A and D pollen types, respectively, and is of more limited value in grouping species under the B and C types. In this respect the concept of pollen types as we have employed it here, is morphological rather than taxonomic.

An effort was made, however, to determine whether any relationship or correlation exists between the different pollen types and the generally accepted taxonomic system. Pearson (1929), in discussing the taxonomy of *Ephedra*, points out that the general habit of the plant is of little value as a systematic character because in most species it is profoundly influenced by environment. As an example he cites *E. distachya* which may occur as a dwarf bush a few inches in height, or may develop into a shrub up to six feet in height. He emphasized that the remarkable degree of uniformity in the vegetative form and anatomical structure of the plant introduces difficulty in the way of separating and grouping the species. The present taxonomic system is one proposed by Stapf (1889) who based his monographic study of the genus on the characteristics of the bracts of the female inflorescence. His study, although extensive, did not include all presently known species of *Ephedra*. A more recent taxonomic revision of the North American species of the genus was presented by Cutler (1939) and some of the South American species were investigated by Hunziker (1949), but no attempt was made to revise the genus as a whole nor to consider the phylogenetic relationships of the American species with those of the old world. The system in use (Stapf, 1889) remains incomplete and there is still great need for a revision of the entire group. Stapf's system is presented here in an effort to determine whether the pollen groups recognized in the present study have any relation to his taxonomic groups within the genus.

Section I. ALATAE. Mature spike dry; bracts more or less indurated along the midrib, otherwise membranous, produced laterally into wing-like expansions.

1. Tropidolepides.<sup>7</sup> *E. alata* (D); *E. strobilacea* (D).

2. Habrolepides. *E. trifurca* (D); *E. torreyana* (C); *E. multiflora* (B).

<sup>7</sup> Designated as tribes by Stapf, these subdivisions of sections are not validly published (Article 5, International Code of Botanical Nomenclature 1956) and should be republished as either subsections or series. They are used here, however, for purposes of comparison.

Section II. ASARCA. Mature female spike dry; bracts slightly hardened, scarcely membranous-winged.

3. Asarca. *E. californica* (B); *E. aspera* (C).

Section III. EPHEDRA (Pseudobaccatae). Mature bracts of female spike often narrowly membranous-margined, at length becoming thick and fleshy.

4. Scandentes. *E. altissima* (B); *E. foliata* (C); *E. fragilis* (C); *E. fragilis* var. *campylopoda* (B).  
 5. Pachycladae. *E. pachyclada* (A); *E. intermedia* (A).  
 6. Leptocladae. *E. helvetica* (A); *E. distachya* (A); *E. monostachya* (A); *E. gerardiana* (A); *E. equisetina* (A); *E. sinica* (A); *E. regeliana* (A).  
 7. Antisyphiliticae. *E. nevadensis* (B); *E. antisyphilitica* (B); *E. americana* (C); *E. gracilis* (D); *E. tweediana* (B); *E. triandra* (D); *E. ochreatea* (C).

It is apparent that our pollen classification scheme shows only partial agreement with Stapf's groups. In the case of the "Pachycladae" and "Leptocladae" of Section III the correlation is good, inasmuch as Type A pollen only occurs throughout the group. Moreover Type A pollen is restricted in occurrence to these two groups in the genus. In Section I, the "Habrolepides" possess intermediate (Types B and C) as well as Type D pollen; while Section II (Asarca) has only intermediate pollen (Types B and C); Section III (Ephedra) is characterized by the presence of all four groups. In the "Scandentes" the intermediate pollen types are found; while in the "Antisyphiliticae" both intermediate and Type D pollen are characteristic.

As a further comparison, the pollen types and the species of *Ephedra* in which they occur are arranged below by major geographical areas.

#### ASIA.

Type A: *E. equisetina*, *E. gerardiana*, *E. major* var. *procera*, *E. monostachya*, *E. pachyclada*, *E. sinica*.

Type B: None.

Type C: *E. foliata*, *E. regeliana*.

Type D: *E. strobilacea*.

#### MEDITERRANEAN REGION.

Type A: *E. distachya*, *E. graeca*, *E. helvetica*, *E. intermedia*, *E. major* var. *villarsii*, *E. vulgaris*.

Type B: *E. altissima*, *E. fragilis* var. *campylopoda*.

Type C: *E. foliata* var. *ciliata*, *E. fragilis*.

Type D: *E. alata*.

#### NORTH AMERICA.

Type A: *E. clokeyi*, *E. coryi* var. *viscida*, *E. funera*, *E. viridis*.

Type B: *E. antisyphilitica*, *E. californica*, *E. pedunculata*, *E. nevadensis*.

Type C: *E. aspera*, *E. nana*, *E. torreyana*, *E. peninsularis*.

Type D: *E. trifurca*.

#### SOUTH AMERICA.

Type A: None.

Type B: *E. chilensis*, *E. tweediana*, *E. multiflora*.

Type C: *E. americana*, *E. andina*, *E. bracteata*, *E. frustillata*, *E. ochreatea*, *E. wraithiana*.

Type D: *E. breana*, *E. gracilis*, *E. rupestris*, *E. triandra*.



From the above material it will be noted that pollen type A is predominantly Asiatic and Mediterranean in range, with only four of the sixteen species possessing Type A occurring in the western hemisphere and all of these in the United States. In contrast to this, five of the seven species bearing Type D pollen occur in the western hemisphere, four being located in South America and one in the United States. Concerning the remaining two species, one, *E. alata*, is North African, the other, *E. strobilacea*, is Asiatic. Among the intermediate groups B and C seventeen of the twenty-four species are found in the western hemisphere.

Insofar as the authors are aware, the fossil *Ephedra* pollen from Long Island represents the first Cretaceous occurrence known from North America. The grains represent an extreme in one of the four morphological types which we propose as characterizing *Ephedra* pollen. Moreover the grains are morphologically indistinguishable from *Ephedra sinica*, an old world species of the Type A group.

*Ephedra* today is predominantly a warm desert-steppe plant restricted to both meteorologically and physiologically dry areas. In North America it extends from the southwestern desert areas of the United States eastward to Texas and south to Mexico. In South America it occurs from the drier parts of Ecuador through western Chile into Patagonia. In Europe it extends along the northern Mediterranean coast in Spain and France and extends north and east into Germany and Hungary. It also occurs along the north coast of Africa, and extends eastward through Afghanistan into western China. According to Gams (1952, cited by Iversen, 1954) it is indifferent to temperature but seems to require both climatic and edaphic dryness. For example, the typical localities of *E. distachya* are warm, but the same species is found in isolated, remote localities in Siberia north to the arctic circle and in the alpine zone in Tibet. This extreme adaptability possibly explains the presence of *Ephedra* in North America and Europe during late glacial time. Gams (1927) further states that it occurs in very dry and open pine woods. This is extremely interesting in view of the association of the fossil material from Long Island with abundant pollen assignable to the Coniferales and Cycadales.

Tchigouriaeva (1954) suggests that an ancestral form of *Ephedra* (*Ephedrites*) evolved by the Jurassic. This conclusion is based on the similarity between modern *E. foliata* pollen and Permo-Triassic remains of the Cordaitales. These Permian cordaitalian remains are ridged pollen grains bearing two bladders. By the Lower Triassic a progressive reduction in bladder development had occurred until the bladders were either vestigial or, in a few cases, completely absent. Tchigouriaeva reasoned, therefore, that by the Jurassic, pollen of the modern *Ephedra* type (without bladders) had probably evolved. It should be noted, however, that no such Jurassic remains have thus far been discovered. Pollen having gnetalian affinities, possessing a varying number of ridges and occasionally a furrow, as in *Welwitschia*, has been described from Cretaceous sediments in Nigeria and Venezuela (Kuyl et al., 1955). Tchigouriaeva's hypothesis is rendered more plausible, however, by the discovery of Cretaceous pollen of essentially

modern structure as demonstrated in this paper. Doubtless future discoveries will bridge the gap between ancestral forms and true *Ephedra* pollen, and clarify more fully the evolutionary story of *Ephedra* in pre-Cretaceous time.

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## EXPLANATION OF PLATES

## PLATE I

FIGS. 1-5. Major morphological types characterizing *Ephedra* pollen grains. FIG. 1. *Ephedra aspera*, Type C. FIG. 2. *Ephedra sinica*, Type A. FIG. 3. *Ephedra distachya*, Type A. FIG. 4. *Ephedra trifurca*, Type D. FIG. 5. *Ephedra californica*, Type B. (All figures  $\times 1200$ .)

## PLATE II

FIG. 1. Modern *Ephedra distachya*. View of the serpentine colpus. Note the primary and secondary branching. FIG. 2. Same grain at mid focus, showing the thickness of the exine in outline. Note also the dissection of the ectexinous ridge crests which are visible in optical section along both edges of the grain. This dissection is caused by branching lateral colpi. FIG. 3. Modern *Ephedra trifurca*. View at high focus of the wide, low, slightly scabrate ridges characteristic of Type D pollen. Note the bright, hyaline furrows. FIG. 4. Same grain at mid focus, showing the thickness of the ectexine. FIG. 5. Modern *Ephedra funera*. High focus view of the straight, slightly verrucate ridges. FIG. 6. Modern *Ephedra americana*. Mid focus view showing the projecting ectexine at the poles. FIG. 7. *E. americana*. A polar view of a similar grain. Note the high but fine, straight ridges and their junction at the poles. (All figures  $\times 1000$ .)

## PLATE III

FIG. 1. *Ephedra californica*. High focus view of the narrow, undulating, hyaline ridges which characterize Type B pollen. FIG. 2. Same grain at mid-focus, showing the outline of the ridges along the edges of the grain. FIG. 3. *Ephedra sinica*. High focus view of the reticulation found along the surface of the exine between the ridge crests. FIG. 4. Same grain at mid-focus, showing the extent of the outline of the endexine. FIG. 5. The undulating ridge along the opposite side of the body is visible. FIG. 6. *E. sinica*. A smaller specimen in which the baculate condition of the ectexine is visible in optical section. (All figures  $\times 1000$ .)

## PLATE IV

FIG. 1. *Ephedra viridis*. High focus view of the angular, undulating colpus. FIG. 2. Same grain at higher focus. Note the smoothness of the ridge crest. FIG. 3. *Ephedra chilensis*. High focus view of the undulant ridge crest. FIG. 4. *Ephedra andina*. Typical Type C pollen grain. FIG. 5. *Ephedra sinica*. Polar view of mid focus showing the structure of the ridge. Note the continuous and evenly distributed endexine, the hyaline central core of each ridge and the thin outer tissue. FIG. 6. Same grain at high focus showing the junction of the ridges at the poles. FIG. 7. *Ephedra nevadensis*. High focus view of the tightly undulant ridge. FIG. 8. *Ephedra aspera*. High focus view of the characteristic straight ridges of Type C pollen grains. FIG. 9. *Ephedra breana*. High focus view of the low, gently domed ridges characteristic of Type D pollen grains. (All figures  $\times 1000$ .)



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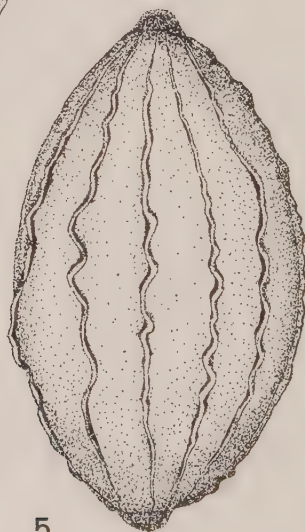
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STEEVES & BARGHOORN, POLLEN OF EPHEDRA



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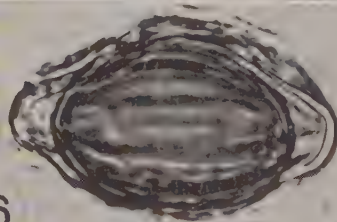
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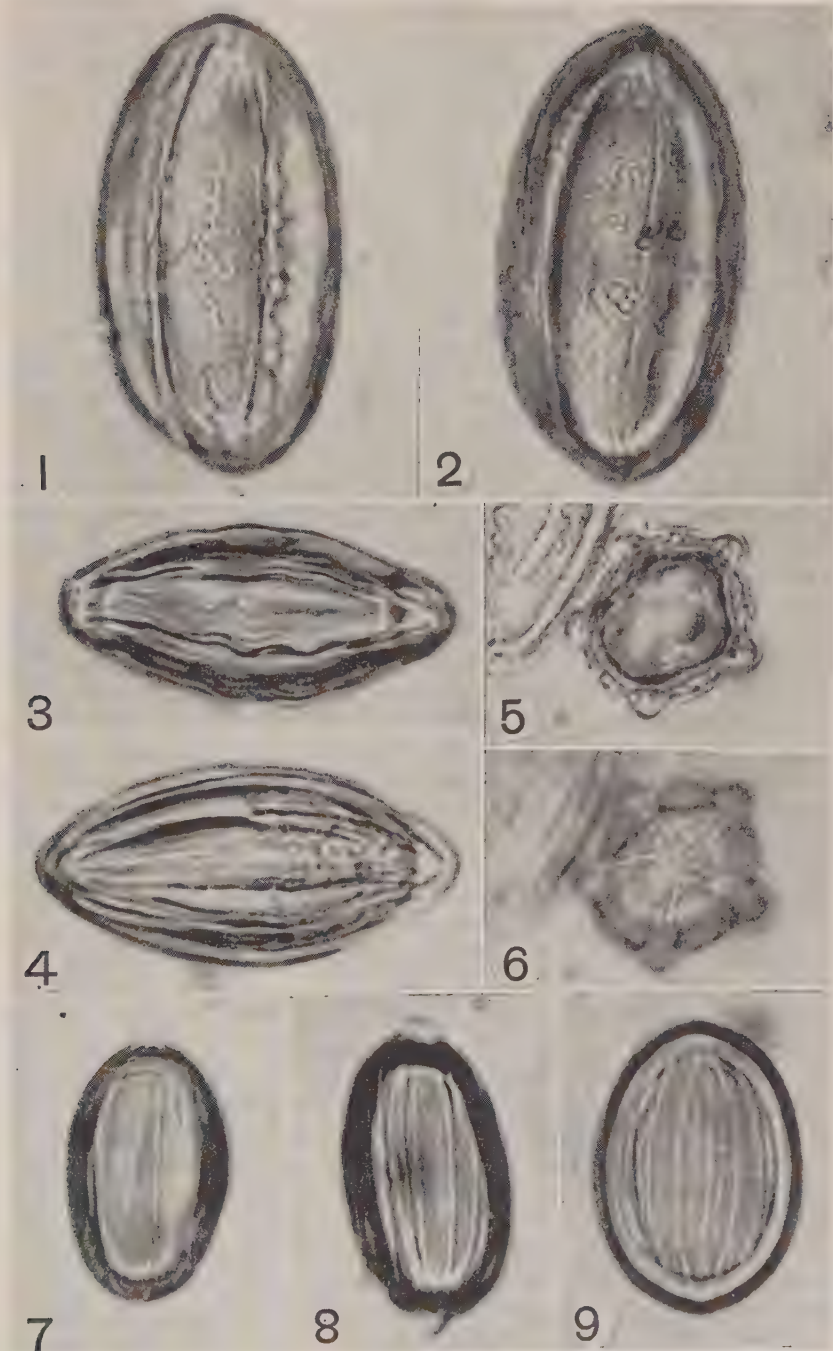


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STEEVES & BARGHOORN, POLLEN OF EPHEDRA



STEEVES & BARGHOORN, POLLEN OF EPHEDRA

## ANATOMICAL STUDIES OF BARK REGENERATION FOLLOWING SCORING

KYAW SOE

SCORING of the trunks or branches of fruit and ornamental trees to induce earlier and more prolific flowering and fruiting has been practised for thousands of years. This method of checking phloem transport is more temporary in its effect than the ancient procedure of ringing or the more recent bark inversion (Sax, 1954), but it is easily done and is less hazardous than either of these practices. If scoring does not inhibit phloem transport long enough to insure maximum response, it can be repeated. In order to determine the duration of the effect of scoring and the nature of bark regeneration, studies were made with both slow- and rapid-growing trees.

Two types of trees were used, the fast-growing silver maple (*Acer saccharinum*) and a hybrid poplar (ex *Populus deltoides*), and the slow-growing apple, 'Prairie Spy,' and the 'Seckel' pear. The maple and poplar trees were three years old while the pear and apple trees were five to six years old. The trunks and branches were scored by cutting with a knife through the bark to, and often into, the underlying xylem. In the earlier experiments, the cuts were made directly around the trunk or branch, but in the later the cut was made in a diagonal spiral to prevent the breakage of branches. Samples of the cut bark and underlying wood were taken every few days after scoring in order to study the regeneration of the severed bark. After fixing, longitudinal radial sections were cut, stained and mounted.

### HISTOLOGICAL TECHNIQUE

Samples removed from the trees were treated in two ways. In most of the cases, the samples were cut into 15–20  $\mu$  sections on a sliding microtome. The majority of the sections were radial longitudinal sections, but cross sections were cut when necessary. For more detailed studies of the material removed from the trees, it was fixed in formalin acetic alcohol (Johanson, 1940). A modified Zirkle's n-butyl alcohol method for dehydration was employed and the paraffin-tissuemat method of Pratt and Wetmore (1951) was used for embedding the material. Just before microtoming, the embedded material was exposed by cutting off the unnecessary paraffin on the required surface and soaked in 50% alcohol for at least three hours before cutting. To avoid curling and to insure easy handling of the sections a thin sheet of polyethylene was used to cover the top of the material before each section was cut. The flattened sections on the polyethylene sheet were mounted on cleared slides smeared with egg-albumen fixative and flooded with 2% formalin.

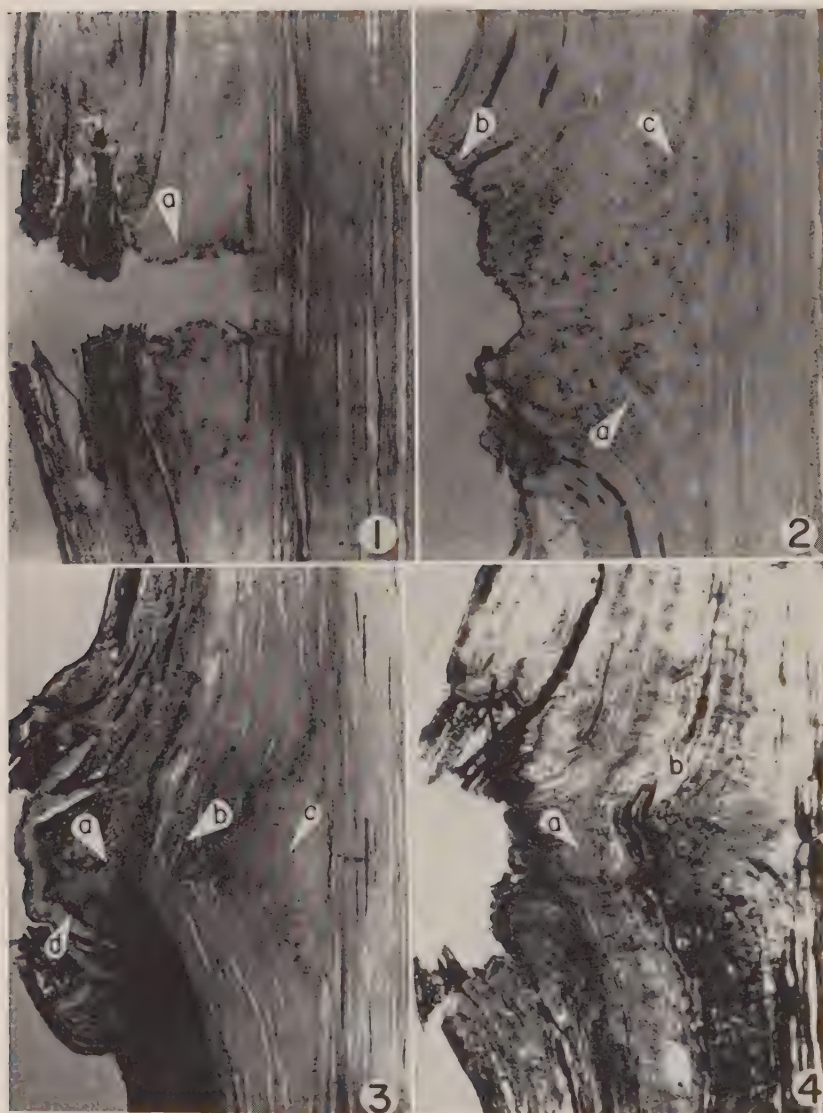
Different stain combinations for studying different elements during the



development of the new bark were used as follows: (a) 1% safranin counter-stained with 0.5% fast green in 100% ethyl alcohol and clove oil (Johanson, 1949); (b) 1% safranin with 2% analin blue in methyl cellosolve; (c) bismark brown, iodine green, resorcin blue (Iacmoid) (Esau, 1948) all diluted 1/5,000 (Esau, 1948).

### OBSERVATIONS

**Poplar.** The three-year-old poplar stem has a thick cortical region and the phellem of the normal bark consists of five to ten years of cork cells. In the phloem, the sieve elements were in patches and were arranged in alternate tangential rows with phloem fibers, each row being of one to eight phloem fibers thick. The cambial zone (vascular) with its immediate derivatives formed a distinct zone. When studied after scoring, it was shown that the ringing reached into the mature xylem two to ten cells (or approximately so) deep. By the third day, the exposed cut surfaces of the wound had dried out, especially the marginal cells in the region of cork, cork cambium, cortex and outer mature phloem cells. Callus formation took place at this stage from two living tissue systems: (a) the living cells of the longitudinal conducting system which includes phloem parenchyma, vascular cambial zone and xylem parenchyma; (b) the horizontal living cells which comprise the vascular rays of the phloem, the vascular cambium, and both immature and mature xylem (FIGS. 5, 6). On the sixth day, there was very active callus formation and the two edges of the callus formed on the upper and lower margins of the cut fused (FIG. 2) and bulged out. The outermost cells of the callus were exposed and dried out. Some of the immature xylem elements near the wounds became mature while callus was forming. They became lignified and were characteristically distorted as they were pushed out by the increasing volume of callus below them, especially the active growth of the vascular ray cells (FIG. 2). Just outside of these lately-formed, distorted xylem elements, a series of cells within the callus developed into a distinct cambial zone which formed a bridge over the cut (FIG. 2). This formation of a new cambial zone began at the regions where the callus tissue met the normal undisturbed cambial zone. At the deepest part of the cut, mature xylem cells characteristically show the lumen filled with cells which closely resemble tyloses. The entrance of these cells into the vessels has not been observed, but all indications seem to point to their being tylose in nature, originating from neighboring ray initials or callus cells formed from such ray initials. Practically every mature vessel in the neighborhood of the bottom of the cut is so filled. While some of the xylem elements became distorted as they matured, the mature phloem which was not taking part in the formation of callus was pushed outward. Some phloem tissue entered into the formation of callus. On the ninth day, it was found that the newly formed vascular cambium had produced new xylem elements of a short and distorted nature towards the inside. Also, phloem elements were formed outwards as usual, and these were also distorted and abnormal in their mor-



FIGS. 1-4. Development of callus and new vascular cambium, cork cambium, phloem and xylem at the region of the cut after scoring.

FIG. 1. Radial longitudinal section of poplar stem at the region of the wound, three days after scoring: a, callus formation is initiated on either side of the wound in the region of immature phloem, vascular cambium and immature xylem ( $\times 24$ ). FIG. 2. Radial longitudinal section of poplar stem at the region of the wound, six days after scoring: a, vascular cambium; b, cork cambium; c, some immature vascular elements become mature after being pushed out by the growth of callus tissue ( $\times 21$ ). Note that the callus tissue from both sides of the wound fuses to form a continuous mass. FIG. 3. Radial longitudinal section of poplar stem sixteen days after scoring: a, region of new phloem; b,

phology. Some sieve-tube elements even showed the presence of callose formation. The phloem fibers, instead of showing their normal elongated form, took the form of rounded sclereids. By this time a new cork cambial layer was well established in the callus region outside of the vascular cambium where it joined the normal cork cambium zone on either side, thereby becoming continuous over the wound. From the twelfth day to the sixteenth day, the xylem elements produced gradually assumed their normal characteristics in size and form, while the newly formed phloem elements were still abnormal in their morphology (FIG. 3). However, on the twentieth day the new vascular system, phloem as well as xylem, and periderm formation became perfectly normal.

**Maple.** In a three-year-old maple stem, the bark is thinner than in the poplar. The observations made on bark regeneration were more or less comparable to those of the poplar. On the third day after scoring, the usual drying of the cells in the exposed area took place in the cork, cork cambium, phloem and even the immature xylem elements. Callus was actively forming by the sixth day; it was comparable to the callus formation of poplar as described. On the ninth day, the two callus masses, one above and one below the wound, fused, and a distinct vascular cambial layer was formed in the callus which united the two edges of the undisturbed vascular cambium. On the twelfth day, the vascular cambial zone was well established and began to produce its derivatives, but no mature vascular elements were found as yet. By the sixteenth day, the mature products of the newly formed vascular cambium became distinct, both xylem and (less distinctly) phloem. Although the earlier-formed xylem elements were short, distorted and irregularly arranged, the later ones became more normal. Newly formed phloem elements were more distorted, irregular in arrangement, and fewer than the newly formed xylem elements. By the twentieth day, the vascular cambium was producing perfectly normal phloem and xylem elements.

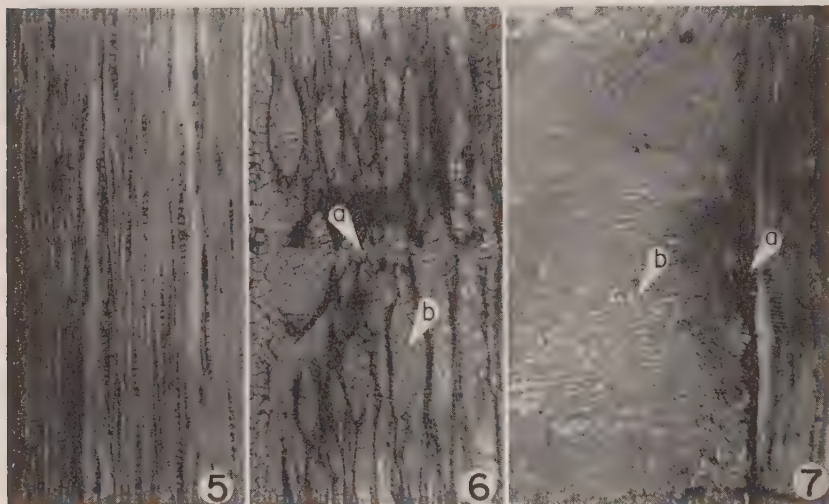
**Apple.** The apple variety we used ('Prairie Spy') had a green bark which was thicker than that of the poplar mentioned above. On the third day after scoring, there was no obvious change, but there was a slight callus formation in the region of immature phloem and xylem along the flanks of the cut. On the sixth day, there was more drying of the exposed edges of the wound and there was a more obvious production of callus which originated in a manner similar to that in the previously mentioned plants. At this time, a layer of living cells which was below the dried cells at the regions of cork cambium, cortex and outer portion of the phloem became active and acted as a new cork cambium. On the ninth day, the callus formation became faster than before and the two edges of

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region of newly formed xylem elements; c, callus cushion between the new and old xylem; d, new cork cambium ( $\times 21$ ). FIG. 4. Radial longitudinal section of stem of apple twenty days after scoring, showing resumption of normal vascular and cork cambial activities: a, region of newly formed phloem; b, region of newly formed xylem ( $\times 18$ ). Compare the amount of callus produced in apple (FIG. 4) with poplar (FIG. 3).



callus tissue fused together. There was a definite cambial zone formed which bridged the cut, but no obvious vascular elements were formed as yet. By then the cork cambium had produced four or more layers of derivatives. On the twelfth day, the callus formation did not show any progress and thus the amount of callus formed did not even reach to the level of the epidermis of the axis (FIG. 4). The hidden small amount of callus which developed and differentiated to produce both cork cambium and vascular cambium in no more time than in the abundant callus of poplar and maple, was very deceptive when one examined the wound superficially. But, remarkably, the vascular cambium had already been producing both phloem and xylem composed of short, distorted and irregularly arranged elements, and by the sixteenth day, the production of normal phloem and xylem was resumed. On the twentieth day, the newly formed vascular cambium and cork cambium were perfectly normal and were producing normal derivatives (FIG. 4).



FIGS. 5-7. Callus development from cells of the rays after scoring. FIG. 5. Tangential longitudinal section of poplar showing the characteristic uniseriate rays of a normal plant ( $\times 36$ ). FIG. 6. Tangential longitudinal section of stem of poplar at the region of the wound, showing the multiseriate ray cells which take a major part in the formation of callus: a, the region of the cut made by the knife in scoring; b, multiseriate ray with large component cells ( $\times 36$ ). FIG. 7. Radial longitudinal section of stem of maple showing callus tissue being derived from the ray cells: a, vascular ray cells continuous with their derivative callus cells; b, callus cells which have divided by successive periclinal divisions to form horizontal rows of callus cells ( $\times 36$ ).

**Pear.** In pear, the nature of bark regeneration was almost the same as the apple. The callus formation began on the sixth day, and it was relatively small in comparison with the poplar and maple. On the twelfth day, the vascular cambium was produced and the new cork cambium was well



established. By this time, the vascular cambium was producing short and distorted vascular elements. By the sixteenth day, the production of the normal vascular tissue was resumed and by the twentieth day, both cork cambium and vascular cambium resumed their normal functions perfectly and produced derivatives which were normal in structure, size and arrangement.

## DISCUSSION

The present investigation indicates that the amount and the rate of callus production in a wounded area following scoring varies in the different plants studied. The source of callus also varies to some extent. In scoring experiments on trees of poplar, silver maple, pear and apple, callus formation is mainly contributed by living cells of vascular rays (Figs. 5, 6, 7) in the proximity of the cut. There is also some evidence that living longitudinally oriented parenchyma cells of phloem, of xylem and of vascular cambium take part in the formation of callus (Fig. 1). If we look at the literature on the source of callus in the regeneration of new bark, well discussed by Bloch (1941), one finds a diversity of opinions on the origin of callus. Sass (1932) in his study of the formation of callus knots on apple grafts showed that it is produced exclusively by tissues located outside of the xylem cylinder. According to him, any living tissue of the bark, excluding the periderm, may proliferate, and the cambium may produce very little callus. On the other hand, Sharples and Gunnery (1933) showed that in their study of the development of callus in the healing of a surface wound produced by an excision of a strip of bark from the stem of *Hibiscus rosa-sinensis* and *Hevea brasiliensis* (1933), the development of the callus cushion is predominantly from the vascular ray system and the cambium takes no part in its early stage of development. It is clear that Sass in his investigation showed the origin of callus from all the living tissues of the bark except periderm, while Sharples and Gunnery showed that the vascular ray cells are the main source for the origin of callus. The latter are supported by observations made in the present investigation (Figs. 5, 6, 7). Both of them agree that the cambium took very little part in callus formation which is also supported by the present investigation.

In this study it was found that new vascular cambium formation took place on the sixth day in poplar and on the ninth day in maple, pear and apple trees. The new vascular cambium formation is usually independent of the amount and the rate of callus production. It was also found that the activity of the new cork cambium started as soon as the wound callus pad is well developed. The formation of cork cambium was always found ahead of the vascular cambium formation in the plants studied.

In the present investigations, the new xylem elements, followed quickly by the new phloem elements, started appearing soon after the formation of the vascular cambium (that is, about on the ninth day) but they were not abundant and all were abnormal and distorted. In some cases, callose material was seen in and near plates of the sieve-tube elements even on

the ninth day. It was only on the twentieth day, or approximately so, that the plants studied showed normal and regular development of xylem and phloem elements. However, as before the scoring, the number of xylem elements produced was naturally more than that of the phloem. It is interesting that the amount of callus formed in poplar and maple was more and appeared earlier than in pear and apple; yet all four produced new phloem and xylem at about the same time. The result of the present investigation on bark regeneration agrees with that of Murneek (1939), in which he states that the branches of apple trees ringed with a wire girdle healed in three to five weeks.

The anatomical studies of spiral ringing in crab apple and branches of other apples showed that the conducting tissue formed by the cambium subsequent to the scoring was changed in orientation so that the long axes of the elements were parallel to the spiral.

### CONCLUSION

Following scoring, the new cambium is formed in about a week, but the complete restoration and functioning of the phloem required about three weeks. If done at an appropriate time of year, a single scoring may check phloem transport long enough to induce flowering and fruiting, but, if not, the process can be repeated every two or three weeks to insure earlier flowering and fruiting of ornamental and fruit trees.

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## THE GENERA OF THE PRIMULEALES OF THE SOUTHEASTERN UNITED STATES \*

R. B. CHANNELL AND C. E. WOOD, JR.

THE FAMILIES Theophrastaceae, Myrsinaceae and Primulaceae which compose the order Primulales are almost universally agreed to be rather closely related. Both Theophrastaceae and Myrsinaceae are woody tropical groups (with few exceptions), while the Primulaceae are primarily of temperate distribution and are herbaceous, apparently approaching the Myrsinaceae most closely through a few woody species of *Lysimachia*. All three groups are held together, however, by the mostly pentamerous and sympetalous flowers; by the androecium of an outer, antesepalous whorl of staminodia (which may be lacking) and an inner, antepetalous whorl of stamens; by the similar pollen; by the unilocular ovary with free-central placentation; and by the bitegmented ovules.

Although in the Englerian sequence of families the Primulales are placed immediately following the Ericales and Diapensiales, the free-central placentation has led various botanists to associate the Primulales with the Caryophyllales (Centrospermae). Cronquist (Bull. Jard. Bot. Bruxelles 27: 25, 26. 1957) has pointed out, however, that difficulties attend the derivation of the woody and tropical Myrsinaceae from the predominantly herbaceous Caryophyllales. "A resort to woody members of the Caryophyllales such as some of the Phytolaccaceae, as possible near-ancestors of the Primulales tends to vitiate the significance of the free-central placentation as an indicator of relationship between the Primulales and Caryophyllales, inasmuch as the genera of the Phytolaccaceae with united carpels have axile placentation. If the Primulales are indeed related to the Caryophyllales it must be through a woody common ancestor with axile placentation or even with separate carpels, and the free-central placentation has been independently achieved in both groups. On the basis of present evidence the Guttiferales meet the qualifications of a possible ancestor of the Primulales at least as well as do any of the Caryophyllales."

Although the Plumbaginaceae are sometimes included in the Primulales, several lines of evidence indicate that the apparent similarities to this group are probably parallel developments. The Plumbaginaceae seem to be treated best as a separate order Plumbaginales, related to but distinct from the Caryophyllales, although they have been placed with this group by Friedrich (Studien über die natürliche Verwandtschaft der Plumbaginales und Centrospermae. Phytion Austria 6: 220-263. 1956).

The familial and generic treatments below follow the general scheme out-

\* Previously published papers in this series include the genera of the woody Ranales (Jour. Arnold Arb. 39: 296-346. 1958), the Nymphaeaceae and Ceratophyllaceae (40: 94-112. 1959), and the Empetraceae and Diapensiaceae (40: 161-171. 1959).



lined in the first paper of this series of studies prepared for a biologically oriented generic flora of the southeastern United States. It may be called to attention again, however, that the area is bounded by and includes North Carolina and Tennessee, Arkansas and Louisiana; that the descriptions are based primarily upon the species occurring within this area, with any supplementary material added for clarity being included in brackets; that the abbreviations used for periodicals follow the useful principles of Schwarten and Rickett (Bull. Torrey Bot. Club 76: 277-300. 1958); and that all references which we have not seen are marked by an asterisk.

This work on the flora of the southeastern United States, which is being conducted as a joint project of the Gray Herbarium and the Arnold Arboretum, has been made possible through the kind support of George R. Cooley and through a grant from the National Science Foundation. The treatments below were prepared originally by the first author in 1957 while he was associated with the Gray Herbarium and the Arnold Arboretum; they have been edited by the second author as a result of the development of a standard format for these studies and have been modified by him through the incorporation of additional material which has been located since that time. In all of this work on the southeastern United States we are greatly indebted to many of our colleagues and friends for their interest and assistance. In connection with the Primulales we are further indebted to George R. Cooley, for temperature data in connection with the effects of the low temperatures in Florida in 1957-1958 (see *Rapanea*), and to Richard A. Eaton, for his assistance in obtaining living specimens of *Hottonia* for illustration. As in the previous papers in this series, the illustrations are the careful work of Dorothy H. Marsh.

#### THEOPHRASTACEAE (JOEWOOD FAMILY)

Shrubs and trees differing from the Myrsinaceae in the biseriate androeium, the outer (antesepalous) whorl staminodial, and by anatomical features, including the absence of secretory elements and the presence of long strands of sclerenchymatous tissue beneath the leaf epidermis. The presence of broad rays in the wood apparently is correlated with the highly dissected nature of the vascular system of the axis. The relationship of these two families is worthy of further anatomical investigation. The fruit of the Myrsinaceae is a 1-few-seeded drupe, usually small and dark brown or black, while that of the Theophrastaceae is usually a large yellow or orange berry, only rarely a 1-seeded drupe. TYPE GENUS: *Theophrasta* L.

A family of four genera, differing in the form and disposition of the staminodia, and about 60 species distributed in the American tropics and Hawaii. Represented with us by a single indigenous species of *Jacquinia*.

*Clavija longifolia* (Jacq.) Mez is sometimes cultivated as an ornamental in the South. Native to Venezuela and Colombia, it is a shrub of *Mahonia*-like habit, attaining a height of 3-5 m. It has large oblong-spatulate to lanceolate, leathery, spinose-toothed leaves and drooping racemes of fragrant, orange or saffron flowers with glandular staminodia.

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1. *Jacquinia* L. Amoen. Acad. 5: 388. 1760, "*Jaquinia*"; L. Sp. Pl. ed. 2. 1: 271. 1762, "*Jaquinia*"; Jacq. Select. Stirp. Am. Hist. 53. 1763; L. Gen. Pl. ed. 6. 101. 1764.

Shrubs or small trees with alternate, simple, persistent, exstipulate leaves without resin ducts. Flowers complete, hypogynous, actinomorphic, 5-merous, gamopetalous. Androecium biseriate: fertile stamens 5, epipetalous at the base of the corolla tube in a single whorl opposite the corolla lobes, the anthers extrorse; staminodia 5, alternating, forming the outer series, petaloid, adnate near the base of the corolla lobes. Gynoecium derived from 5 carpels but appearing simple: ovary unilocular with a central free placenta and several anatropous 2-integumented ovules embedded in the mucilaginous matrix filling the ovary cavity; style and stigma 1. Fruit a dry berry. Seeds few, with well developed embryo and copious endosperm. TYPE SPECIES: *Jacquinia ruscifolia* Jacq. (= *J. aculeata* (L.) Mez). (Generic name in honor of Nicolaus Joseph Jacquin, 1727-1817, distinguished Austrian botanist, sent by Emperor Francis I to the West Indies to procure plants for the Imperial Garden at Schoenbrunn, of which he later became director.) — JOEWOOD, CUDJOEWOOD.

A tropical American genus of about 25-30 species, of which a single one, *Jacquinia keyensis* Mez (*J. armillaris* sensu Chapm. non Jacq.), occurs in our area. Our plant is a compact, symmetrical shrub or small tree with a round-topped crown of yellowish green foliage, attaining a height of about 5 meters. It is characteristically a strand species, distributed in our area in dry coastal hammocks of southern peninsular Florida, on calcareous rock of the Everglade Keys and the Florida Keys, and beyond our region in the Bahamas and Hispaniola. The obovate or cuneate-spatulate coriaceous leaves, usually notched at the apex, have entire, revolute margins and are often clustered at the ends of the brittle, sclerose-tomentose twigs. The very fragrant yellowish or straw-colored flowers are produced in racemes at the ends of the twigs, primarily in winter. The fruits are borne on erect or ascending, bracteate pedicels and are pointed with the base of the persistent style.

*Jacquinia armillaris* Jacq. (*J. Barbasco* Mez), a native of the West Indies, is sometimes cultivated in Florida as an ornamental. Resembling *J. keyensis* in foliage, this species has white flowers with scarious-margined, non-ciliate sepals and red fruits.

## REFERENCE:

SARGENT, C. S. *Jacquinia*. Silva N. Am. 5: 155-158. pl. 242. 1893.

## MYRSINACEAE (MYRSINE FAMILY)

Shrubs or trees, mostly with alternate, simple, entire, exstipulate, glandular-punctate leaves, in ours persistent. Flowers 4–6-merous, regular, usually hypogynous, complete or polygamo-dioecious, variously disposed, often clustered on scaly spurs or in panicles or cymes. Calyx shorter than the corolla, the sepals imbricate, connate at the base, persistent. Corolla rotate or short-salverform, the lobes united at the base or sometimes distinct. Stamens distinct, in a single whorl adnate to the corolla tube opposite the lobes, the anthers [transversely or] longitudinally dehiscent; staminodia absent. Pistil 1, derived from 4–6 carpels but appearing simple: ovary 1-loculed, bearing few to many semi-anatropous or semi-campylotropous ovules buried in a fleshy-proliferated axile or basally attached free central placenta filling the ovary cavity. Fruit in ours a 1-seeded drupe, usually dark colored, the seed with a cylindrical embryo and copious endosperm. (Including Ardisiaceae.)

A relatively large family of about 32 genera and approximately 1000 species widely distributed in the tropics and subtropics; two indigenous species in our area, representing two of the largest genera, both of subfam. MYRSINOIDEAE Pax, characterized by the superior ovary and the 1-seeded fruits.

The Myrsinaceae and the Theophrastaceae are distinguished from the Primulaceae by their woody habit, the indehiscent 1–few-seeded drupaceous or berry-like fruits and the fleshy or pulpy, sometimes mucilaginous placenta surrounding or embedding the ovules. The Myrsinaceae differ from the Theophrastaceae by the absence of staminodia and by anatomical features enumerated under the latter family.

The pollen grains of the Myrsinaceae are usually 3(–5)-colpor(oid)ate, suboblate to prolate, more or less similar to those of Primulaceae and Theophrastaceae.

The family is of limited economic importance. It is the source of several ornamental shrubs.

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## KEY TO THE GENERA OF MYRSINACEAE

- Ovules multiseriate (Tribe ARDISIEAE); inflorescences terminal, manifestly paniculate, the pedicels slender, longer than the flowers or fruit; flowers conspicuous, the corolla lobes reflexed; style slender; stigma entire. . . . . 1. *Ardisia*.  
 Ovules in a single circumferential series (Tribe MYRSINEAE); inflorescences ap-

pearing as congested cymes scattered along the twigs on scaly spurs, the pedicels 1–2 mm. in length, shorter than the flower or fruit; flowers inconspicuous, the corolla lobes erect or spreading; style short; stigma lobed.  
 ..... 2. *Rapanea*.

Tribe ARDISIEAE A. DC.

1. *Ardisia* Swartz, Prodr. Veg. Ind. Occ. 48. 1788, nom. cons.

Shrubs or small trees, the flowers of our species conspicuous, in terminal panicles, the pedicels slender, articulate at the base, the corolla rotate, 5 (rarely 4–6)-parted, the lobes convolute in the bud or sometimes one wholly exterior, recurved at anthesis. Stamens distinct, erect, connivent in a column around the style; anthers sagittate at the base, pointed at the apex, dehiscent by slits, the filaments equalling the anthers in length. Style linear, exceeding the anthers; stigma entire. Fruit a drupe, the endocarp longitudinally ribbed, bony. (Including *Icacorea* Aubl. 1775, nom. rejic.) TYPE SPECIES: *Ardisia tinifolia* Swartz. (Name from Greek *ardis*, point, apparently referring to the apiculate-tipped stamens of some species.) — MARLBERRY, MARBLEBERRY, CHERRY.

A large genus of about 250 species, mostly tropical. Represented with us by a single indigenous species of subgenus *ARDISIA* (subg. *Pickeringia* (Nutt.) Mez). *Ardisia escallonioides* Cham. & Schlecht. (*A. Pickeringia* Nutt., *Icacorea paniculata* (Nutt.) Sudw.) is a common small tree of coastal hammocks of southern Florida, extending northward along about two-thirds of the east coast of the peninsula and about one-half of the west, and occurring inland to some extent in moist hammocks and in the hammocks and pinelands of the Everglade Keys and Florida Keys. Beyond our area it is most abundant in the Bahamas, Cuba and Hispaniola, less frequent in Mexico and Central America. In Florida the marlberry commonly grows in the shade of other trees, the small crown of leaves often elevated to 3 m. or more. The white, purple-streaked, fragrant flowers appear in abundance in paniculate clusters at the ends of the leafy twigs, usually about November. The globose, shining, black fruits, about 7–8 mm. in diameter, mature more or less throughout the year. The long, linear styles are often persistent in fruit.

*Ardisia polycephala* Wall. (subg. *TINUS* (Burm.) Mez), native to Burma, has been reported to occur in hammocks and around old homesteads in southern Florida as an escape from cultivation. This species has axillary clusters of white or pinkish flowers with contorted corolla lobes and slender-tipped anthers. The nearly black fruits are about 1 cm. in diameter. Although persisting, this shrub does not appear to spread to any significant extent.

*Ardisia crenata* Sims (*A. crispa* sensu A. DC. and many others, not *A. crispa* (Thunb.) A. DC.), of subg. *CRISPARDISIA* Mez, and *A. japonica* (Hornsted) Blume, of subg. *BLADHIA* (Thunb.) Mez, both natives of eastern Asia, are used rather extensively as horticultural ornamentals for their foliage and showy red berries.



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## Tribe MYRSINEAE Pax

2. *Rapanea* Aubl. Hist. Pl. Guiane Franç. 1: 121. pl. 46. 1775.

Shrubs or small trees, the flowers small, inconspicuous, congested-umbellate, on short, scaly axillary spurs scattered along the twigs, the pedicels short. Corolla spreading or rotate, 5-parted, the tube short. Stamens with ovate-oblong anthers, nearly sessile. Style obsolete, shorter than the stamens; stigma lobed. TYPE SPECIES: *Rapanea guianensis* Aubl. (Name derived from a native name for the plant in French Guiana.)

About 140 species of tropical and subtropical distribution in both hemispheres. *Rapanea guianensis* (*Myrsine Rapanea* Roem. & Schult., *Myrsine floridana* A. DC.) occurs in coastal hammocks of southern peninsular Florida as far north as Volusia County on the east coast and Levy County on the west, in hammock "islands" in the Everglades, on the Everglade Keys and the Florida Keys. It is distributed through tropical America to southern Brazil and Bolivia, being most common in the West Indies, less frequent or rare in Mexico. The flowers and fruits are borne on short spurs along the branches, as in species of *Myrica*, and fruiting specimens bear a very close superficial resemblance to *M. inodora* Bartr., even the foliage being comparable. The globose fruits are dark blue or black in color and at maturity are about 4 mm. in diameter, capped by the persistent sessile stigma. The oblong-obovate leaves, 4-10 cm. long, are mostly clustered at the ends of the branchlets.

The unusually cold winter of 1957-1958 provided various examples of the effects of low temperatures on tropical and subtropical genera. *Rapanea guianensis* which was seen in abundance in April 1958 in Gulf Hammock, near Chassahowitzka, Citrus County, not far from the apparent northern limit of the species on the west coast of Florida, had been killed to the ground by the cold of the winter (temperatures of 15° F. reported locally) but was sending out abundant sprouts from the bases of the plants. Severe winters such as this undoubtedly are one of the primary factors involved in determining the northern limit of this species.

## PRIMULACEAE (PRIMROSE FAMILY)

Annual, winter-annual or perennial herbs [or very rarely shrubs] with alternate, opposite or whorled simple leaves and regular, complete, hypogynous or (in *Samolus*) perigynous, 4-8-merous flowers. Stamens as many as the gamopetalous corolla lobes, epipetalous, inserted opposite the lobes on or at the base of the tube, sometimes with as many alternating stami-

nodia, the filaments sometimes connate, the anthers introrse, longitudinally dehiscent. Pistil 1, compound (as indicated by the valves of the ovary); ovary 1-locular with a free-central placenta arising from the base and bearing several to many amphitropous or anatropous ovules; style 1, glabrous; stigma terminal, usually slightly dilated. Fruit a valvate or circumscissile capsule [or rarely indehiscent]. Seeds several to many, with a small embryo in fleshy albumen.

A family of about 20 genera and approximately 500 species, widely distributed in the Northern Hemisphere, occurring on all continents but most abundant in the north-temperate regions.

The Primulaceae are distinguished by their predominantly herbaceous habit, gamopetalous corollas, epipetalous stamens in a single whorl opposite the corolla lobes, free-central placentation and valvate or circumscissile capsules with numerous seeds.

Vascular evidence indicates that the unilocular condition of the ovary of the Primulaceae, with free-central placentation, is of a derivation similar to that of the Caryophyllaceae; the primulaceous flower is descended from an ancestor having a plurilocular ovary with axile placentation. Several modern systematists have suggested that the primitive condition may well be found among the Centrospermae. However, evidence from the remainder of the plant has not yet been adequately considered.

Generic relationships within the Primulaceae are not clear. Consequently, several different tribal arrangements exist for the family. Objections have recently been raised to the alliance (on the basis of the reflexed corolla lobes) of *Dodecatheon* with *Cyclamen* and the resultant separation of these genera from *Primula*. *Dodecatheon* has been considered on anatomical grounds to approximate more closely the original primulaceous flower than any of the other family representatives, but evidence based upon chromosome numbers raises some question in this regard. *Lysimachia* has also been suggested as the most primitive genus of the family and that nearest the Myrsinaceae, for some species of sect. *Apodanthera* (cf. *L. solanoides* Hand.-Mazz.) are lignescent, with indehiscent or hardly dehiscent capsules, and subsessile, upright anthers which open by terminal pores. There has been no recent study of the problem of generic relationships within the Primulaceae taking into consideration evidence from all available sources.

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*machia vulgaris*, *Anagallis arvensis*, *Primula vulgaris* and *Samolus Valerandi*.]

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#### KEY TO THE GENERA OF PRIMULACEAE

- A. Terrestrial or marsh plants with entire or merely toothed leaves; flowers solitary, umbellate or racemose.
- B. Ovary wholly free from the calyx.
- C. Scapose; flowers in involucrate umbels.
- D. Low, rosulate annuals with pubescent leaves; corolla inconspicuous, the lobes erect or spreading at anthesis; calyx accrescent, the lobes green, not ridged, the tube whitish and prominently ridged; stamens distinct, included. . . . . 1. *Androsace*.
- D. Perennials with broad, glabrous or glabrate leaves; corolla conspicuous, the lobes reflexed at anthesis; calyx herbaceous, not ridged, the lobes and tube similar in texture; filaments connate below, the anthers forming an exerted cone. . . . . 2. *Dodecatheon*.
- C. Caulescent; flowers solitary in the leaf axils or in racemes.
- E. Stem with scale-like alternate leaves below and a single whorl of thin, lanceolate leaves at the summit, subtending the pedunculate, 6–8 (mostly 7)-merous flowers; corolla white. . . . . 4. *Trientalis*.
- E. Stem leafy throughout, leaves alternate, opposite or whorled; flowers 4–6-merous.
- F. Capsule valvate; corolla yellow; perennials with opposite or whorled leaves; flowers 5–6-merous. . . . . 5. *Lysimachia*.
- F. Capsule circumscissile; corolla scarlet, blue or white; annuals with alternate or opposite leaves; flowers 4–5-merous. . . . . 6. *Anagallis*.
- B. Ovary partially inferior, adnate to the calyx tube; inflorescence racemose, the pedicels bracteate or ebracteate. . . . . 7. *Samolus*.

A. Aquatic plants with pectinately dissected leaves; flowers in whorls on the conspicuously inflated, floating peduncles. . . . . 3. *Hottonia*.

1. *Androsace* L. Sp. Pl. 1: 141. 1753; Gen. Pl. ed. 5. 69. 1754.

Small, scapose, pubescent annuals [biennials or perennials, these scapose or caespitose]. Leaves ovate-lanceolate, sparingly denticulate [or quite various]. Scapes 1-many, the inflorescence a simple umbel [or scapes single-flowered]; flowers involucrate, borne on unequal pedicels. Calyx accrescent, the whitish tube broadly ridged, the 5 lobes green and not ridged. Corolla small, white, marcescent, included within the calyx, the lobes obtuse, shorter than the tube [or in perennials surpassing the calyx and conspicuous]. Stamens 5, the anthers oval to oblong, the short filaments attached at or below the middle of the corolla tube. Style short, the stigma capitate-disoid, the ovary superior, ovoid to globose. Capsule valvate to the middle, coriaceous above, membranaceous below. Seeds many, small, blackish. TYPE SPECIES: *Androsace carnea* L. (A name applied by Pliny to some unknown plant.)

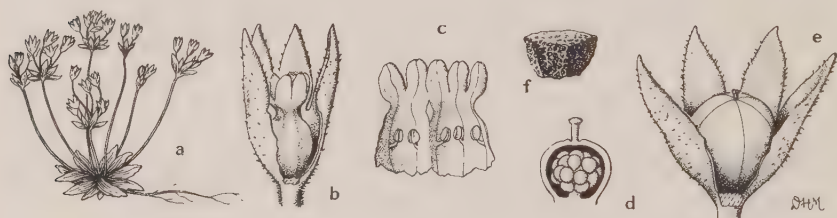


FIG. 1. *Androsace*. a-f, *A. occidentalis* Pursh var. *occidentalis*: a, habit,  $\times \frac{1}{2}$ ; b, flower with one sepal removed,  $\times 5$ ; c, corolla opened to show stamens,  $\times 5$ ; d, pistil, semi-diagrammatic, the ovary in vertical section,  $\times 10$ ; e, mature fruit and calyx, one sepal removed,  $\times 5$ ; f, seed,  $\times 10$ .

About 85-90 species, chiefly of the mountainous and boreal-arctic regions of Eurasia, but with six species and six varieties, all of sect. *CHAMAEJASME* Koch (sensu Handel-Mazzetti), in North America. The genus barely enters our range in Washington County, Arkansas, where *Androsace occidentalis* Pursh var. *occidentalis* has been collected. This variety with erect or somewhat spreading calyx lobes and erect to arched-ascending pedicels, has a wide range, primarily in the western United States (Mississippi, Missouri, and Arkansas river valleys, foothills of the Rocky Mountains in Colorado, Utah and Montana and into southwestern British Columbia, and also in the mountains of New Mexico and Arizona) in dry sands, gravels and rocky woods. Var. *arizonica* (Gray) St. John, with spreading to arched-reflexed calyx lobes and filiform pedicels, is restricted to the mountains of southeastern Arizona.

The marcescent corollas, often exhibiting a narrow constriction of the tube below the lobes, are inconspicuous in the annual species and are not



used taxonomically in this group; here the primary characters are those of calyx and capsule.

Chromosome numbers of  $2n = 20$ , and 72 have been reported for two Old World species.

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#### 2. *Dodecatheon* L. Sp. Pl. 1: 144. 1753; Gen. Pl. ed. 5. 71. 1754.

Scapose perennial herbs chiefly of calcareous soils. Leaves lanceolate or oblanceolate, entire, the inflorescence a naked scape bearing a simple, involucrate umbel, the pedicels erect in bud, somewhat recurved or arched at anthesis, erect in fruit. Calyx 5-lobed, the lobes equalling or longer than the tube, reflexed at anthesis, erect in fruit. Corolla white or purplish, 5-parted, the tube short, the lobes oblong, erect in bud, reflexed at anthesis. Stamens 5, erect, the filaments short, separate or united into a tube, the anthers basifixed, much longer than the filaments, connivent around the style, the connective prominent, smooth. Stigma slightly if at all dilated, exserted beyond the stamens; style filiform; ovary ovoid, equaling the filaments at anthesis. Capsule ovoid or cylindric-conical, much longer than the calyx, thick-walled, valvate; seeds numerous, spherical or ovoid, ours without membranaceous edges, reticulate, anatropous. TYPE SPECIES: *Dodecatheon Meadia* L. (The name from the Greek *dodeca*, twelve, and *theos*, god, given by Pliny to another plant, probably the primrose, which was allegedly under the care of the twelve superior gods.) — SHOOTING-STARS, AMERICAN COWSLIPS, MEADIAS.

A North American genus of about 15 species, mostly western. Section DODECATHEON, to which our species belongs, differs from sections PURPUREO-TUBULOSA Knuth and CAPITULUM H. J. Thompson by a combination of characters, including the nondilated stigma, valvate capsule (as opposed to operculate), the yellow (rarely dark), separate or united filaments and the seeds without membranaceous margins. There are also developmental differences in the seedlings of the three sections: the first true roots in sect. DODECATHEON develop from the hypocotyl just below ground level, well below the cotyledons; in sect. PURPUREO-TUBULOSA from a subterranean carrot-shaped caudex; and in sect. CAPITULUM from the aerial hypocotyl at the base of the cotyledons.

*Dodecatheon Meadia* has been variously treated taxonomically. Fassett recognized 5 varieties, some of dubious taxonomic significance, based primarily on quantitative characters of stamen-tube, calyx-lobe and capsule dimensions. Thompson has more recently recognized only three units:

subsp. *Meadia* ( $2n = 88$ ), subsp. *brachycarpum* (Small) Knuth and subsp. *membranaceum* Knuth, the first two of which occur within our area.

Subspecies *brachycarpum* (var. *brachycarpum* (Small) Fassett) (Virginia to northern Georgia, Tennessee, Missouri, Oklahoma and Texas) is characterized by small flowers and fruits. Throughout its range it is sympatric with subsp. *Meadia* with which it intergrades wherever the two come into contact. The latter, however, occurs northward to Wisconsin well into the area of glaciation. Within glaciated territory morphological variation in this species is unimodal, while outside this area variation is bimodal, suggesting the presence of two populations. Populations within glaciated territory are, however, more variable as to flower color than those of unglaciated areas.

The third, subsp. *membranaceum* (var. *Frenchii* Vasey), is restricted in distribution to southern Illinois, adjacent Kentucky and the driftless area of Wisconsin. Characteristically a plant of overhanging, wet or dripping cliffs, where it grows in dense shade, it is characterized morphologically by the abrupt contraction of the leaf blade into the petiole. It occurs within the extensive range of subsp. *Meadia*, which has considerably thicker, noncordate blades. Specimens of the two subspecies have occasionally been found growing within a few feet of one another, although they are easily distinguished morphologically. Ecological experiments, including reciprocal transplantation in the field, as well as greenhouse observations, indicate no change in leaf form as a result of varying light intensities and support the genetical and morphological distinctness of the two taxa.

With the exception of var. *Frenchii* Vasey (subsp. *membranaceum*), the five varieties of *Dodecatheon Meadia* recognized by Fassett on morphological grounds do not occupy different environments. Based primarily on quantitative characters of stamen-tube, calyx-lobe and capsule dimensions, these varieties are of dubious taxonomic significance. Solution of the problems of variation in this complex would appear to require genetic studies.

The taxonomic characters utilized in this group vary considerably. Collectors should record corolla color in the field and such other characters as may be obscured in pressing. The varying shape of the connective and the connation of the filaments have been found to be unreliable as taxonomic characters but no one has suggested the cause of such variation. The red color at the base of the leaves of *D. Meadia* is not lost in herbarium material; in pressing this color consistently disappears from the leaves of *D. radiculatum* Greene (*D. amethystinum* Fassett), a species of the East but one apparently not represented in our area. Fruit-texture and -color are reported to be reliable both in the field and in the laboratory.

Although insects have occasionally been observed to visit the flowers of *Dodecatheon*, their role in pollination is unknown. The structure of the flower suggests that self-pollination is frequent, if it is not the primary means of pollination. The observations of collectors in this respect would be helpful. The flower buds are at first erect, but, during anthesis when the sepals and petals are reflexed, the pedicels arch outward and downward,

placing the flowers in a nodding position. The erect anthers surrounding the exserted style are thus inverted and, upon dehiscence along their connivent surfaces, a certain amount of pollen falls upon the stigma. In fruit the pedicels reassume an erect position.

The reported chromosome numbers form a polyploid series ( $2n = 44, 66, 88, 132$ ).

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### 3. *Hottonia* L. Sp. Pl. 1: 149. 1753; Gen. Pl. ed. 5. 72. 1754.

Aquatic herbs with pectinate leaves scattered along the rooting and floating stem and crowded in a whorl beneath the cluster of conspicuous, inflated aerial peduncles; the pedicellate flowers and subtending sepeloid bracts whorled at the constricted nodes, forming interrupted racemes. Calyx of 5 herbaceous, linear-oblong sepals. Corolla white, 5-lobed, the lobes as long as or shorter than the tube. Stamens 5, the filaments short, adnate near the center of the corolla tube; pollen 3-colporoidate. Stigma minutely clavate; style linear; ovary subglobose. Capsule obpyriform to subglobose, membranaceous, 5-valved, the valves sometimes coherent at base and apex; seeds numerous, small, oblong-oval, longitudinally rugose, anatropous. TYPE SPECIES: *Hottonia palustris* L. (The name in honor of Petrus Hotton, 1648–1709, Dutch botanist and professor at Leiden.) — FEATHERFALL, WATER-VIOLET.

Two species, the Eurasian *Hottonia palustris*, and *H. inflata* Ell. of the eastern United States. *Hottonia inflata* is widespread, but of sporadic occurrence, from Florida to Texas and north to New England, New York, Ohio, Indiana, southern Illinois and Missouri. In most areas it is considered rare, although it sometimes occurs in abundance. In New England the species is a winter annual, with the seeds germinating in autumn and the

seedlings growing rapidly. Although growth is retarded during the winter months, the plants survive protracted periods beneath a cover of ice. By May the plants reach the surface of the water and the inflated peduncles develop. The flowers appear from late May to mid-June. After flowering, the old plants shed the pectinate leaves and decay as the seeds ripen.



FIG. 2. *Hottonia*. a-g, *H. inflata*: a, flowering and fruiting plant,  $\times \frac{1}{4}$ ; b, flower with bract,  $\times 5$ ; c, corolla, opened to show stamens,  $\times 5$ ; d, pistil, semi-diagrammatic, the ovary in vertical section,  $\times 5$ ; e, mature fruit,  $\times 5$ ; f, pedicel and placenta from a large fruit near base of inflorescence, after dehiscence of fruit,  $\times 5$ ; g, seed,  $\times 15$ .

Structural and functional dimorphism is reported for *Hottonia palustris* ( $2n = 20$ ) from the British Isles. Pollen grains of the long-styled flowers differ in size as compared with those of short-styled flowers by a proportion of 14 to 9, respectively. (Cf. *Pontederia*.) The significance of the size differences is unknown. Pollination experiments with short-styled flowers indicate that the species is at least partially self-fertile when artificially pollinated. Manual cross-pollination of short-styled flowers with pollen from a long-styled individual of a different source also effects seed production, with a considerably larger proportion of fruit and seed set than in the former instance, suggesting that the heterostylous condition is of functional significance in promoting cross-pollination. In contrast, *Hottonia inflata* exhibits neither heterostyly nor other structural dimorphism. Although the style is quite short, at anthesis the stigma reaches the included anthers and is often seen to be covered with pollen from the same flower, suggesting that self-pollination frequently occurs in this species.

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4. *Trientalis* L. Sp. Pl. 1: 344. 1753; Gen. Pl. ed. 5. 161. 1754.

Low, nearly smooth, rhizomatous, perennial herbs of woodlands and peaty slopes, spreading by slender, elongate stolons. Stems simple, erect, bearing several inconspicuous alternate bracts and a conspicuous whorl of lanceolate, acuminate, thin-textured, veiny leaves at the summit and a few axillary, slenderly pedunculate, star-shaped, delicate white flowers. Flowers (6)7(8)-merous. Calyx deeply parted, the lobes linear-lanceolate. Corolla deeply parted, rotate, the lobes ovate-elliptic, pointed, coherent at the base as a short, nearly obsolete tube. Stamens with slender filaments, united basally in a short ring on the base of the corolla, the anthers oblong, basifixed, revolutely coiled in anthesis. Stigma only slightly dilated; style filiform, equalling the filaments; ovary globose, about equalling the corolla tube at anthesis. Capsule globose, valvate to the base, the valves recurved, exposing the several grayish-granular seeds persisting temporarily upon the erect placenta. TYPE SPECIES: *Trientalis europaea* L. (The name from the Latin *triens*, one-third of a foot, alluding to the height of the plant.) — STARFLOWER, CHICKWEED-WINTERGREEN.

Three species of the North Temperate Zone, only one barely entering our area in northeastern Tennessee. *Trientalis borealis* Raf. (*T. americana* Pursh) is distributed from Labrador to Saskatchewan, south to Newfoundland, Nova Scotia, New England, Virginia, West Virginia, Tennessee, Ohio, Illinois and Minnesota. It occurs in shady woodlands southward and on peaty slopes northward, ascending to subalpine regions. *Trientalis latifolia* Hook. occurs in the montane and subalpine regions of Pacific North America from western California into British Columbia. *Trientalis europaea* L. var. *europaea* ( $2n =$  ca. 112 or 160) is primarily Eurasian; var. *arctica* (Hook.) Ledeb. enters North America from western Siberia, extending from the Bering Strait and the Aleutians to the mountains of Oregon. Similar in habit, these species differ in the shape of leaves and corolla lobes. *Trientalis* is closely related to *Lysimachia*.

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5. *Lysimachia* L. Sp. Pl. 1: 146. 1753; Gen. Pl. ed. 5. 72. 1754.

Rhizomatous, caulescent, perennial herbs [or rarely shrubs] of decumbent or repent habit and with simple, opposite or whorled (sometimes glandular-punctate) entire leaves. Flowers 5, 6(7)-merous, variously disposed. Calyx herbaceous, of 5 deeply parted imbricate or valvate lobes. Corolla yellow [or white] rotate or somewhat campanulate, of 5 deeply parted, convolute or individually supervolute lobes and a short tube, sometimes with as many alternating staminodia. Filaments of the fertile stamens nearly distinct or united at the base, the 2-loculed anthers basifixed or somewhat versatile. Stigma terminal; style linear; ovary ovoid to globose. Capsule 5-valved, the seeds few to many, oblong, orbicular or angular, sometimes winged, the embryo in evident endosperm. [ $2n = 18, 20, 24, 28, 30, 36, 60$ , in species beyond our range.] (Including *Steironema* Raf.) TYPE SPECIES: *Lysimachia vulgaris* L. (Named, according to tradition, for King Lysimachus of Thrace, who, when confronted by an enraged bull, waved a loosestrife before it and quieted it; or from the Greek *lysis*, a release, and *mache*, strife, alluding to ancient lore which attributed to the plants the power of conciliation in animals.) — LOOSESTRIFE.

A genus of about 160 species in seven subgenera, of wide distribution, especially in the northern hemisphere (with the largest number of species in eastern India, northern Burma and southern China). Fourteen species, in two subgenera, occur in our area. At various times most of the subgenera have been considered to be independent genera, but on a world-wide basis there seems to be no positive evidence for such separation.

Subgenus SELEUCIA Bigelow (*Steironema* Raf.), with evident staminodia, arose or apiculate corolla lobes supervolute in bud (each inclosing a stamen), and epunctate leaves, includes five species of temperate America north of Mexico, all in our area. The continental-ranging *L. ciliata* L. is closely related to *L. tonsa* (Wood) Knuth, of the southern Appalachians. *Lysimachia radicans* Hook., primarily of the lower Mississippi embayment but with stations in Virginia, approaches *L. lanceolata* Walt., centered in the eastern United States and with two intergrading subspecies, *lanceolata* (including *L. heterophylla* Michx.) and *hybrida* (Michx.) J. D. Ray (var. *hybrida* (Michx.) Gray). Especially distinctive is *L. quadriflora* Sims, mostly of the north-central states but with stations in at least Georgia and Arkansas in our area.

Subgenus LYSIMACHIA (subg. *Cassandra* Bigelow), characterized by absence of staminodia, imbricate corolla lobes with entire margins, and punctate leaves, is a large and complex group centering in southeastern Asia, with only five indigenous American species. Section NUMMULARIA (Gilib.) Klatt includes the repent, very floriferous, but usually sterile and apparently apomictic, *L. Nummularia* L. ( $2n = 36$ ), introduced from Europe, and, to the north of our area, *L. punctata* L. ( $2n = 30$ ), also of European origin. Section LYSIMACHIA (sect. *Lysimastrum* Endl.) is composed of only the distinctive *L. Fraseri* Duby, of the mountains of North Carolina, Georgia, Tennessee and Alabama, the European *L. vulgaris* ( $2n = 28$ ), nat-

uralized in the northern United States and Canada, and *L. salicifolia* F. Muell., of Australia. Section TRIDYNIA (Raf.) Gray includes the widespread *L. quadrifolia* L., primarily of woodlands, its close relative *L. asperulifolia* Poir., restricted to the Carolina coastal plain, *L. Loomsii* Torrey, with a similar distribution in the Carolinas and Georgia, and *L. terrestris* (L.) BSP., of wide northern distribution and unique in producing axillary bulblets. The fertile *L. × producta* (Gray) Fern. and the sterile *L. × commixta* Fern. are the putative hybrids of this last with *L. quadrifolia* and with *L. thyrsiflora* (subg. NAUMBURGIA), respectively.

Recently evaluated on a morphological basis, some of our species of *Lysimachia* are well marked and easily identified; others are believed to hybridize to a greater or lesser extent and present patterns of variation which are often difficult to interpret. Cytological and genetic investigations would appear to be a source of useful information on the relationships among the variable species.

The generic status sometimes accorded subgenus SELEUCIA (as *Steironema* Raf.) is based in part upon the presence of staminodia. Various interpretations as sterile filaments and as mere nonvascular excrescences, in the two species studied anatomically these structures as primordia show vascular traces, but there is no further development of the vascular tissue. The floral anatomy of all of the species thus far examined is fundamentally the same, and, except for the presence of staminodia, species of *Steironema* fall naturally into the genus *Lysimachia*.

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6. *Anagallis* L. Sp. Pl. 1: 148. 1753; Gen. Pl. ed. 5. 73. 1754.

Low, erect, spreading or procumbent annual herbs with alternate or opposite entire leaves and peduncled or nearly sessile flowers solitary in the leaf axils; plants of sandy fields, low grounds, damp sands and mud. Corolla (4)5-lobed, conspicuous (rotate with almost no tube) and deciduous, or inconspicuous (the urceolate or globular tube equalling the lobes) and often marcescent at summit of the capsule. Stamens (4)5, the filaments bearded or glabrous, adnate at the base or near the middle of the corolla tube. Ovary ovoid, the style linear, the stigma minutely capitate; capsule membranaceous, globose, circumscissile near the middle, the seeds numerous, angular. (Including *Centunculus* L., *Micropyxis* Duby.) TYPE SPECIES: *Anagallis arvensis* L. (The ancient Greek name, probably from *ana*, again, and *agallein*, to delight in, alluding to the habit of the flowers of opening again in the sunlight after having closed in cloudy weather.) — PIMPERNEL, SCARLET PIMPERNEL, POOR MAN'S WEATHER GLASS.

About 24 species, mostly native to the Mediterranean region, Africa and South America, three widely distributed. The three species known from the United States, representing two of three subgenera, occur within our area.

Subgenus ANAGALLIS, including plants with conspicuous, nearly rotate corollas and opposite or whorled leaves, is represented in our area by *Anagallis arvensis* L. ( $2n = 40$ ), native to the European-Mediterranean region but now a widespread weed on nearly every large land mass. The species includes three subspecies, two of which are known from the United States. Subspecies *arvensis* (subsp. *phoenicea* (Scop.) Vollmann) includes plants with scarlet, salmon, white, lilac, or blue corollas, with relatively large lobes, and comparatively smooth margins, fringed with numerous



gland-tipped, 3-celled trichomes. Subspecies *coerulea* (Schreb.) Vollmann (subsp. *foemina* (Mill.) Schinz & Thellung) comprises plants with blue flowers with narrower and smaller corolla lobes which are denticulate-margined and only sparsely glandular with 4-celled hairs. Both scarlet and blue forms of subsp. *arvensis* are well known in the United States. Subspecies *coerulea*, apparently less common, occurs at least in Illinois and Texas and may be expected within our area. Corolla color, rarely indicated, is difficult to determine in dried materials and should be noted by the collector. All blue-flowered plants should be examined carefully while fresh for the small, but important, distinguishing details. The corollas of both subspecies have a purple center produced by cells with purple sap in which small, blue, spicular crystals are aggregated.

Both subsp. *arvensis* and subsp. *coerulea* have been studied in considerable detail. The color variants of subsp. *arvensis* form an interfertile series which shows Mendelian segregation in the hybrids. Subsp. *coerulea* is partially isolated genetically and produces sterile  $F_1$  hybrids with all except the salmon form of subsp. *arvensis*. The  $F_1$  offspring of this last cross have pink flowers and are fully fertile. Segregation for flower color and other characters occurs in the  $F_2$ .

The relationship to these of the third, subsp. *gentianeae* (Beck) Domac, requires further study. As delimited by Domac (1956), the subspecies includes plants with gentian-blue flowers, the petals of which are almost intermediate between those of the other two subspecies in shape, size and margin, and which are densely beset with 3-celled trichomes like those of subsp. *arvensis*. Trichomes of the stamen-filaments are 8–10 (mostly 9)-celled while those of subsp. *arvensis* are 5–8-celled and those of subsp. *coerulea* are 11–12-celled. Although all of the specimens cited by Domac were from Yugoslavia, the distribution is probably much wider.

*Anagallis arvensis* is an obligate long-day plant, continuing in vegetative growth indefinitely with less than the critical 12-hour light period. Cross-pollination in this species is by Hymenoptera and Diptera. The flowers are also adapted to self-pollination, however, and are fully self-fertile.

Subgenus CENTUNCULUS (L.) P. Taylor, primarily a group of tropical Africa and one traditionally treated as a genus, includes species which combine characters of erect habit, alternate leaves, terminal inflorescences, small, pale flowers, subpersistent corollas and glandular ovaries. In the widespread *A. minima* (L.) Krause (*Centunculus minimus* L.) ( $2n = 22$ ) the corolla is very short and the stamens are connate and adnate to the corolla for about half their total length. The pantropical *A. pumila* Sw. (*Micropyxis pumila* (Sw.) Duby; *Centunculus pentandrus* R. Br.), composed of three varieties, is represented with us by var. *pumila*, confined to low grounds of peninsular Florida. The corolla is longer and the stamens are connate and adnate less than a quarter of their total length (except in *A. pumila* var. *djalonis* (A. Chev.) P. Taylor, of tropical Africa), as in the remainder of the subgenus and genus. Inasmuch as the adnation is merely a matter of degree and varies within a single species, the retention of *Centunculus* as a genus seems unjustified.

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7. *Samolus* L. Sp. Pl. 1: 171. 1753; Gen. Pl. ed. 5. 78. 1754.

Caulесcent or subscapose, somewhat succulent, glabrous, perennial herbs with alternate, simple, entire leaves, typically of wet situations in sand, sandy loam or muck, occurring also in salt marshes and on almost bare, eroded limestone. Inflorescences racemose, the wiry pedicels with or without bracts. Calyx herbaceous, campanulate, the 5 triangular lobes acute or acutish, equal to or longer than the adherent tube. Corolla white or pinkish, 5-lobed, the tube shorter or longer than the lobes, the throat sometimes glandular-pubescent. Stamens 5, included, sometimes with alternating staminodia. Stigma terminal, sometimes capitate; style linear; ovary ovoid, half-inferior. Capsule subglobose, the 5 valves thick-textured above, thinner below; seeds small, numerous, angular. (Including *Samodia* Baudo ex Small.) TYPE SPECIES: *S. Valerandii* L. (The name probably of Celtic origin, said to refer to curative properties of the genus in diseases of cattle and swine.) — WATER-PIMPERNEL, MARSH-PIMPERNEL, BROOKWTFED.

About ten species, four in North America, the others in the extratropical regions of the southern hemisphere; represented with us by at least two species.

The American representative of the nearly cosmopolitan *Samolus Valerandii* complex, the white-flowered *S. parviflorus* Raf. (*S. floribundus* HBK.), of shallow water and wet soils, is widespread from British Columbia, southern Ontario and Quebec and New Brunswick, southward throughout the United States into Mexico, Cuba and Hispaniola. What is apparently the same species also occurs in southern Brazil, Uruguay, Paraguay, Bolivia, Argentina and Chile. The pedicels are bracteate and the corollas bear staminodia alternate with the stamens. Varying considerably in habit and variously treated taxonomically, the American plant is, in general, more widely and diffusely branched than *S. Valerandii*, with lateral instead of ascending pedicels and setaceous instead of linear-lanceolate bracts. Only the European plant has been investigated cytologically; the  $2n$  chromosome number has been reported to be ca. 24 and ca. 36. The pollen grains are 3-colporoidate and subprolate. The development of the embryo has been followed in considerable detail.

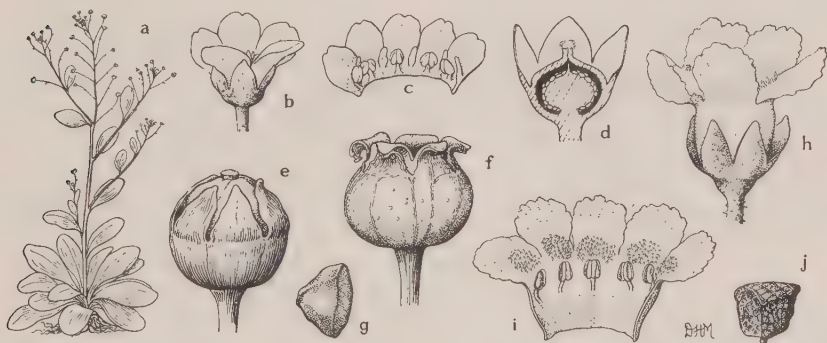


FIG. 3. *Samolus*. a-g, *S. parviflorus*: a, habit,  $\times \frac{1}{4}$ ; b, flower,  $\times 5$ ; c, corolla opened to show stamens and staminodia,  $\times 5$ ; d, flower with corolla removed, the pistil in vertical section,  $\times 10$ ; e, mature fruit before dehiscence,  $\times 10$ ; f, fruit after dehiscence,  $\times 10$ ; g, seed,  $\times 20$ . h-j, *S. ebracteatus*: h, flower,  $\times 4$ ; i, corolla opened to show stamens and patches of glandular hairs,  $\times 4$ ; j, seed,  $\times 20$ .

The pink-flowered *Samolus ebracteatus* HBK., lacking floral bracts and staminodia, grows equally well in sand or sandy loam or on almost bare limestone. Thus considerable variation exists in the extent of development of the stem-system and in leaf-shape, flower-size and the form of the inflorescence. Distributed in the West Indies, Florida, Oklahoma, Texas and Mexico, the species is restricted in our area to the southern tip and western coast of peninsular Florida, presumably dispersed from the West Indies. The cause of the gap in distribution between Florida and Texas and Oklahoma is not known. On rich soils the foliage develops a deeper or brighter green; on limestone the foliage is pale or glaucous and sometimes coated with lime.

*Samolus alyssoides* Heller and *S. cuneatus* Small, both described from Texas, are doubtfully distinct. Glandular-pubescent inflorescences, sup-

posedly characteristic of the latter, appear in populations of *S. ebracteatus* in Florida. The former species is based upon quantitative characters of dubious taxonomic significance. The status of these taxa needs critical evaluation.

The perigynous floral condition characteristic of *Samolus* has been investigated anatomically in *S. parviflorus*. The perianth is firmly attached to the ovary wall, producing an inferior ovary and consequent modification of the perianth pattern. The lower half of the hypanthium is a compound structure consisting of ovary wall and perianth combined. Early anatomical stages show a zonal development of five projecting points which form carpellary walls and five bulbous portions at their bases which unite in forming the central placenta. Ontogenetically the separation between carpel wall and placenta occurs in the embryonic stages and the placenta originates from the fusion of the five basal growing points. A similar situation has been described in *Lychnis* (Caryophyllaceae).

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AND

THE ARNOLD ARBORETUM



## THE CYTOGENETICS OF FACULTATIVE APOMIXIS IN MALUS SPECIES

KARL SAX

SOME OF THE ASIATIC SPECIES OF *Malus* produce predominantly maternal progeny, even when surrounded by other species which bloom at the same time. Since apple species and varieties are generally self-sterile, the production of uniform progeny from trees surrounded by other species or varieties would indicate that these trees are apomictic. The production of occasional variants and the production of occasional hybrids following artificial cross-pollination indicate that apomixis is facultative in these species.

Among the facultative apomicts are *Malus sikkimensis* from northern India, the related *M. rockii* from western China, *M. toringoides* and *M. hupehensis* from China and *M. sargentii* from Japan.

Several of these apomictic apple species are excellent ornamental trees, and *M. toringoides* and *M. sargentii* are usually propagated from seed. For many years the apomictic *Malus* species have been tested as rootstocks for ornamental and horticultural apple varieties. If such seedlings proved to be compatible with the clonal varieties they would provide uniform rootstocks without the expense and long period of time needed to obtain uniform rootstocks by vegetative propagation.

During the past twenty years we have used seedlings of *Malus sikkimensis* as rootstocks for apple varieties. They have proved to be compatible with all ornamental and commercial varieties of apples tested, and for some varieties they are semi-dwarfing. The first seedlings used were from a tree (AA No. 17459) which was raised from seed obtained from the Royal Botanic Gardens, Kew, England, in 1902. The progeny were relatively uniform with only an occasional variant. Unfortunately this tree was cut down before chromosome counts were obtained. The only other source of seed until recent years was a seedling of AA 17459 which was planted in 1936 (AA 50-36-A). Seedlings from the daughter tree proved to be much more variable than those of the original tree.

*Malus rockii* in the Arnold Arboretum is represented by a tree (AA 8334) grown from seed obtained from the University of California Botanic Garden in 1936. Like *M. sikkimensis* it is slow to come into fruit, and seed has been available only during the past few years. The two-year-old trees in the nursery are very uniform, varying only in size and vigor.

*Malus hupehensis* (AA 7441) has given the most uniform progeny of all the species tested, but the seedlings are not very compatible when budded with horticultural apple varieties. The occasional variants are usually dwarf forms.

The oldest tree of *M. toringoides* in the Arboretum (AA 17475) is from seed collected in China by Wilson in 1908. It has produced relatively uni-

form progeny and mature seedlings grown on the Peter Bent Brigham Hospital grounds are duplicates of the mother tree. But seeds sent to Stern in England produced a variant with larger fruit, which was given the varietal name *macrocarpa*. This variety, which is represented in the Arnold Arboretum (AA 11246), flowers about a week earlier than does the mother tree. Seedlings of var. *macrocarpa* grown at the Case Estates of the Arnold Arboretum by Dr. Wyman proved to be very variable in size and, in the several which have borne fruits, these differ in size and shape from either the species or the variety.

The oldest specimen of *M. sargentii* (AA 4681) in the Arnold Arboretum was grown from seed collected in Japan by Sargent in 1892. The variety *rosea* originated as a seedling of the species grown in the Rochester Park. A specimen (AA 11045) was planted in the Arnold Arboretum in 1921. Both *M. sargentii* and var. *rosea* produce 90 per cent or more of maternal-type seedlings when open pollinated. The variants usually differ from their parents primarily in size and vigor. Seedlings of the variety are more vigorous and are more compatible when budded with horticultural varieties than are the seedlings of the species. The variety is being tested as a dwarfing rootstock.

Chromosome counts of these apomictic species and their progeny have been obtained from meiotic divisions of the pollen mother cells and from somatic tissue. The mitotic divisions were obtained from parenchyma cells developed from the medullary rays. A strip of bark was removed from the trunk or branch of the tree and the exposed wood was covered with a strip of polyethylene film. The parenchymatous tissue from the medullary rays develops rapidly and after five or six days can be cut off in thin ribbons and fixed in alcohol-acetic fixative and stained in aceto-carmine. Although the large parenchyma cells provide much better chromosome figures than do root-tip or leaf-tip smears, exact counts are difficult or impossible in the triploids and tetraploids. In most cases the somatic counts reported are accurate to  $\pm 1$  or 2. Meiotic counts, particularly in the triploids, are also subject to some error, because of variation in the degree of pairing of the meiotic chromosomes and the great irregularity of meiosis in most of the triploids.

A summary of the chromosome counts is shown in TABLE I. The seedling of the original specimen of *M. sikkimensis* grown in the Arnold Arboretum is a triploid, but it produces both triploid and tetraploid progeny. A meiotic anaphase of one of the tetraploid progeny is shown in FIG. 1. Two seedlings of one of the tetraploid segregates grown in the Bussey Orchard (BO 4), were examined for chromosome counts and both were found to be triploid. The tetraploids generally have larger flowers and fruits than do the triploids and bloom earlier in the spring.

*Malus rockii* is a tetraploid and relatively good meiotic figures were obtained (FIG. 2). At the first meiotic division there are often several univalents, but the division is quite normal. The seedlings of *M. rockii* grown in the nursery included both tetraploids and, apparently, pentaploids, although only 76 chromosomes could be found in the somatic figure illus-

trated (FIG. 12). Some of the somatic counts reached 85, but exact counts were impossible.

TABLE I. Chromosome Counts of Facultatively Apomictic *Malus* Species and their Progeny

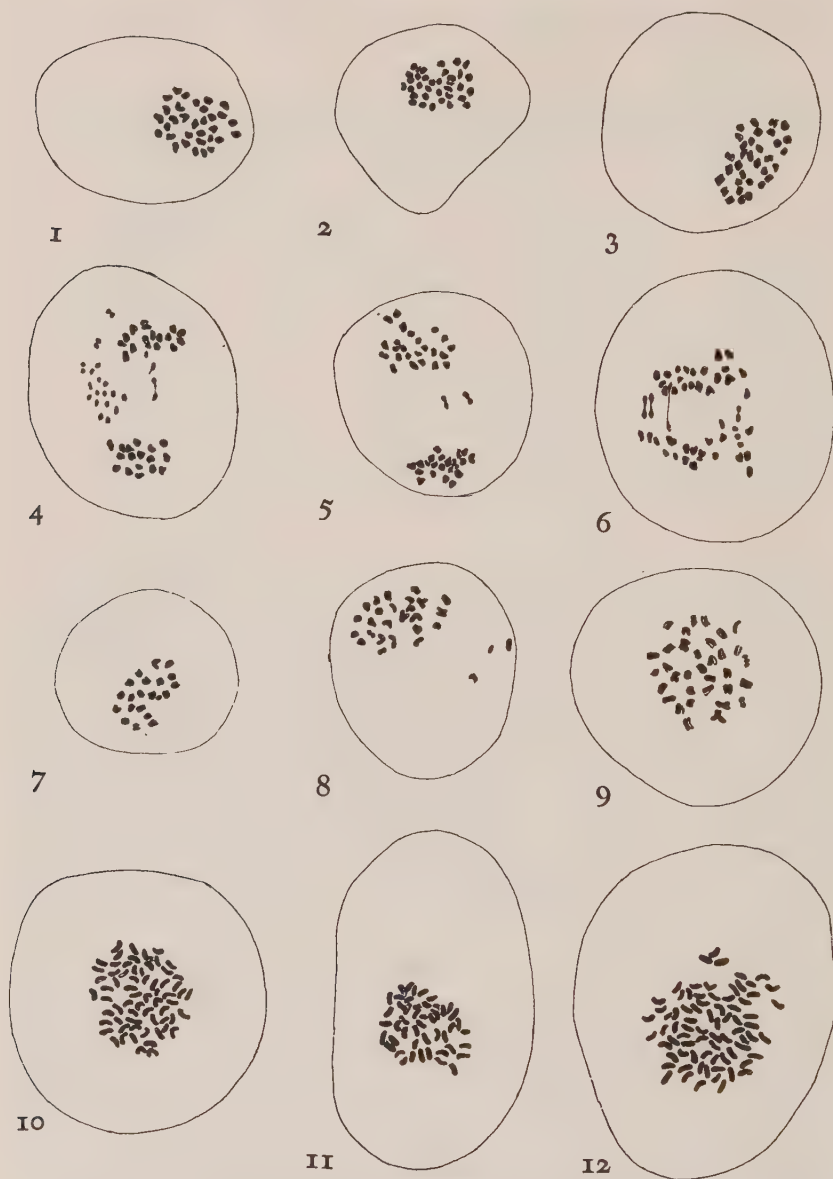
SPECIES	RECORD NUMBER OF		CHROMOSOME NUMBERS		
	SEED PARENT	SEED PARENT	3n	PROGENY 4n	5n
<i>M. sikkimensis</i>	AA 17459	?	1	7	
<i>M. sikkimensis</i> sdlg.	BO 4	4n	2		
<i>M. rockii</i>	AA 8334	4n		4	2
<i>M. hupehensis</i>	AA 7441	3n			
<i>M. toringoides</i>	AA 17475	3n			
var. <i>macrocarpa</i>	AA 11246	4n	6		
<i>M. sargentii</i>	AA 4681	4n		3	
var. <i>rosea</i>	AA 11045	3n	3		

*Malus hupehensis* is a triploid, as determined from meiotic counts by Dermen (1936) and from our somatic counts. Meiosis in the pollen mother cells is very irregular; the tetrads disintegrate and no mature pollen grains are formed. Among the seedlings of *M. hupehensis*, Dermen found two tetraploids in 39 seedlings, based on somatic counts in root tips.

*Malus toringoides* also has very irregular meiotic divisions of the pollen mother cells and stages from prophase to tetrads can be found in a single anther. No critical counts could be obtained from meiotic figures, but somatic counts show that this species is a triploid. The var. *macrocarpa*, however, is a tetraploid, as determined from both meiotic and somatic counts. Meiosis in the tetraploid is normal with only occasional lagging univalents. All the seedlings of the variety which were examined were triploids.

*Malus sargentii* is a tetraploid with about 34 chromosomes at meiosis (FIG. 3) and 68 chromosomes at mitosis. The seedlings from the Arnold Arboretum trees are also tetraploids, but the fact that this species gave rise to the triploid var. *rosea* indicates that some triploid segregates would be found if enough seedlings were grown. The var. *rosea* is a triploid with many univalents at the first meiotic division (FIG. 4). Only three seedlings of the variety were examined cytologically and all were triploids. It is probable that some of the larger progeny of var. *rosea* are tetraploids, but these were not examined.

Many hybrids have been made between *M. sargentii*, or var. *rosea*, and diploid ornamental apples to combine the dwarf growth habit of this species with the superior flowering and fruiting characters of the ornamental diploid varieties. Crosses have also been made with 'McIntosh' as the first step in combining the disease resistance of *M. sargentii* with the fruit size and quality of 'McIntosh.' *Malus sargentii*, or its var. *rosea*, when artificially



FIGURES 1-12. Meiotic and mitotic chromosomes of *Malus* species and hybrids. 1, *M. sikkimensis*, meiotic anaphase I, 32 chromosomes. 2, *M. rockii*, meiotic anaphase I, 35 chromosomes. 3, *M. sargentii*, meiotic metaphase II, 33 chromosomes. 4, 5, *M. sargentii rosea*: 4, meiotic anaphase I,  $3n$ ; 5, meiotic anaphase I,  $3n$ . 6, *M. sargentii rosea*  $\times$  'McIntosh' (5750), meiotic anaphase I,  $3n$ . 7, *M. sargentii rosea*  $\times$  *arnoldiana* (4650), meiotic anaphase I, 21 chromosomes. 8, *M. sargentii rosea*  $\times$  *astracantha* (33340), meiotic anaphase I,  $3n$ . 9, *M. sargentii rosea*  $\times$  *astracantha* (33340 seg.), meiotic metaphase II,  $4n$ . 10, *M. sargentii*



pollinated with pollen of a diploid produces from 0 to about 25 per cent of sexual hybrids. Most of the progeny are maternals in all crosses.

The hybrids were grown to maturity and their progeny from open-pollinated seeds were tested for breeding behavior. Most of them tend to breed true, with a small proportion of variants, indicating that facultative apomixis is a dominant character. The cytology and breeding behavior of the *M. sargentii* hybrids is summarized in TABLE II.

The pollen parents were diploid species and varieties which, when open pollinated, produced extremely variable progeny. Hybrid 19039 ('Henrietta Crosby') is a cross between *M. arnoldiana* (*M. floribunda*  $\times$  *M. baccata*) and *M. pumila* var. *niedzwetzkyana*; 20139 is *M. arnoldiana*  $\times$  *M. purpurea* f. *eleyi* (*M. pumila* var. *niedzwetzkyana*  $\times$  *M. atrosanguinea*); and 6639 is an open-pollinated segregate of *M. spectabilis* f. *riversii*. *Malus astracanica* is a hybrid between *M. pumila* and *M. prunifolia*, and the Hopa Crab is *M. baccata*  $\times$  *M. pumila* var. *niedzwetzkyana*. As would be expected, the progeny of these hybrids are very variable.

The sexual hybrids produced by crossing *M. sargentii* with 19039 or 20139-2 are triploids, as might be expected (FIG. 5). However, when pollinated with 20139-1 or 20139-3, *M. sargentii* produced aneuploid hybrids with the chromosome number near the diploid level. Hybrid 5650-2 had about 21 bivalents with only occasional univalents (FIG. 7). These hybrids lacked vigor and did not live long.

Crosses between the triploid *M. sargentii* var. *rosea* and the diploid species produced progeny ranging from near-diploid to tetraploid. The hybrid between var. *rosea* and *M. astracanica* was a triploid (FIG. 8). Progeny of this hybrid (33340) produced both triploids and tetraploids (FIG. 9). The tetraploid had larger flowers and fruits and bloomed earlier than did the original hybrid.

When crossed with *Malus arnoldiana*, *M. sargentii* var. *rosea* produced an aneuploid with about 17 bivalents and several univalents at meiosis. An aneuploid also resulted when var. *rosea* was crossed with 6639, but two sister hybrids were approximately triploid. Crosses with 'McIntosh' produced a triploid (FIGS. 6, 11), and three tetraploids or near tetraploids (FIG. 10). Crosses with Hopa Crab produced a tetraploid and two feeble aneuploids.

Progeny tests of the *Malus sargentii* F<sub>1</sub> hybrids indicate that facultative apomixis is a dominant character. The F<sub>1</sub> trees were grown in test plots with diploids and the open-pollinated seeds of the hybrids were presumably pollinated with pollen of both diploids and polyploids, although pollen fertility in the triploids is low. The seeds were stratified and grown in flats in the greenhouse. Some of the progenies were transferred to the nursery for further observation and selection. The percentage of variants was somewhat higher when the progenies were scored as young seedlings,

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var. *rosea*  $\times$  'McIntosh' (5750-B), mitotic metaphase, 67 chromosomes. 11, *M. sargentii* var. *rosea*  $\times$  'McIntosh' (5750), mitotic metaphase, 48 chromosomes. 12, *M. rockii* segregate, mitotic metaphase, 76 chromosomes.

because some of the variants were weak plants which did not survive or were too small to transfer to the field. In the field there was some variation in size and vigor of the maternal types. The variant seedlings differed from the maternal type in leaf characters and growth habit and generally were quite variable. The proportion of maternals and variants produced by some of the hybrids is shown in TABLE II.

All of the triploids and most of the tetraploid hybrids produced predominantly maternal progeny when open pollinated. However, one of the tetraploid hybrids between *M. sargentii* var. *rosea* and 'McIntosh' produced twice as many variants as maternals. The tetraploid segregate of *M. sargentii* var. *rosea*  $\times$  *M. astraanica*, 33340, also produced a high proportion of variants, as did the tetraploid segregates of the triploid species *M. sikkimensis* and *M. toringoides*. Yet the tetraploid *M. sargentii*, when open pollinated, produces nearly 100 per cent of maternals.

TABLE II. Cytogenetics of *Malus* Species Hybrids

CROSS	RECORD NUMBER	CHROMOSOME COUNTS		PROGENY SEGREGATION	
		MEIOTIC	MITOTIC	MATERNAL	VARIANTS
<i>Malus sargentii</i>	AA 4681	4 <i>n</i>	4 <i>n</i>	+	
$\times$ 19039	4751-1	3 <i>n</i>	3 <i>n</i>	40	2
$\times$ 20139-2	4851-1	3 <i>n</i>		12	0
$\times$ 20139-2	4851-2	3 <i>n</i>			
$\times$ 20139-1	5650-1	16-17 <sub>II</sub> + 1-3 <sub>I</sub>			
$\times$ 20139-1	5650-2	20-21 <sub>II</sub> + 1-3 <sub>I</sub>			
$\times$ 20139-3	5650-3	16-17 <sub>II</sub> + 1-3 <sub>I</sub>			
<i>M. sargentii</i>					
var. <i>rosea</i>	AA 11045	3 <i>n</i>	3 <i>n</i>	259	24
$\times$ <i>astracanica</i>	33340	3 <i>n</i>	3 <i>n</i>	25	2
Segregate of 33340		4 <i>n</i>	4 <i>n</i>	28	14
$\times$ <i>atrosanguinea</i>	17039	3 <i>n</i>		72	3
$\times$ <i>arnoldiana</i>	4650-3	17 <sub>II</sub> + 3 <sub>I</sub>			
$\times$ 6639	5150-0	22 <sub>II</sub>			
$\times$ 6639	5150-1	3 <i>n</i>			
$\times$ 6639	5150-2	3 <i>n</i>			
$\times$ 'McIntosh'	5750-1	3 <i>n</i>	3 <i>n</i>	16	1
$\times$ 'McIntosh'	5750-2	4 <i>n</i>	4 <i>n</i>	8	16
$\times$ 'McIntosh'	5750-A	4 <i>n</i>	4 <i>n</i>	17	2
$\times$ 'McIntosh'	5750-B	4 <i>n</i>	4 <i>n</i>	33	1
$\times$ Hopa Crab	4450-A	17 <sub>II</sub> + 2-3 <sub>I</sub>			
$\times$ Hopa Crab	4450-B	4 <i>n</i>		72	4
$\times$ Hopa Crab	4450-C	18-20 <sub>II</sub> + 0-4 <sub>I</sub>			

## DISCUSSION

The facultatively apomictic species of *Malus* include both triploids and tetraploids. The triploids usually produce maternal progeny, presumably as the result of the development of an unfertilized and unreduced egg cell.

The occasional production of tetraploids by triploids would indicate that the unreduced egg cell was fertilized by pollen from a neighboring diploid species. The tetraploid species may breed true with only an occasional variant, as in *Malus sargentii*, but in the tetraploid forms of *M. sikkimensis* and *M. toringoides* the progeny are variable with respect to their morphological characters and, in *M. toringoides*, most or all of the segregates are triploids. Apparently the seeds of *M. sargentii* are derived from an unreduced egg cell, while in the tetraploid forms of *M. sikkimensis* and *M. toringoides* they are often, or perhaps usually, produced from the union of a reduced egg cell and a haploid gamete from pollen of a neighboring diploid species.

The sexual hybrids would tend to resemble the mother plant since in the triploids descended from a tetraploid female parent the latter would contribute two of the three genomes, in the tetraploid descended from a triploid female parent the latter would contribute three of the four genomes, while in the pentaploid *M. rockii* segregates the maternal parent would contribute four of the five genomes. Only in the triploids descended from tetraploid female parents would there be genetic segregation due to the reduction division in megasporogenesis, and then only if the tetraploid is heterozygous.

Often the facultatively apomictic tetraploids may produce some triploids, while the triploids may produce tetraploids, and both types of polyploids will have the major characters of the species. Thus chromosome counts from one or a few individuals may not reflect the true cytological picture. It is probable that this condition may be found in other genera of the Pomoidae. The diversity of types in some of the apomictic species of *Cotoneaster* and *Crataegus*, for example, could be the result of such chromosome irregularities.

In the controlled pollination crosses between the tetraploid *M. sargentii* and diploid species and varieties, the production of triploid hybrids was not unexpected (in view of the breeding behavior of open-pollinated triploid species) but the occurrence of near diploids was not expected. The triploid var. *rosea* also produced some near diploids. Apparently both forms of *M. sargentii* produce some egg cells with near diploid chromosome numbers. It is possible that such near-diploid segregates are produced in open-pollinated segregates, but are eliminated or discarded in the young seedling stage.

Triploid apples crossed with diploids normally produce aneuploid segregates with chromosome numbers ranging from diploid to triploid, regardless of whether the triploid is the female or the male parent, indicating that the triploid parent produced gametes with chromosome numbers ranging from 17 to 34 (Wanscher, 1939). The distribution of chromosome counts of the progeny indicates normal chromosome distribution with the most frequent gametic contributions from the triploid in the 23–25 chromosome classes.

As a result of random distribution of the chromosomes in the meiosis of sexual triploids, the progeny of triploids crossed by diploids usually includes very few diploids or tetraploids, and segregates with 40–42 somatic

chromosomes are the most frequent. Yet the triploid *M. sargentii* var. *rosea*, when crossed with diploids, produced tetraploids, triploids and aneuploids near the diploid level in about equal frequencies. Meiosis in the triploids is irregular and could produce egg cells ranging from haploid to diploid, but meiosis in the tetraploid *M. sargentii* does not indicate much irregularity. There is no evidence from microsporogenesis that the tetraploid could produce microspores with one, two or three genomes such as Gottschalk (1958) has described in tetraploid tomatoes. Yet *Malus sargentii* pollinated with diploid species does produce a few hybrids near the diploid level. Apparently megasporogenesis is more irregular than microsporogenesis in these *Malus* species; however, it has not been studied cytologically.

In the progeny of tetraploid *M. sieboldii* crossed with diploid species, Olden (1953) found an occasional diploid or near diploid segregate, some triploids, and an occasional pentaploid. Although *M. sieboldii* usually produces tetraploid maternals, chromosome reduction can occur to produce near haploid or diploid egg cells and the unreduced egg cell can also be fertilized. Even in cultivated clonal varieties of apples, Einset (1952) finds that diploids may produce triploids and triploids may produce tetraploids by the functioning of unreduced egg cells fertilized by haploid male gametes. More recently he has obtained pentaploids from tetraploids.

Some of the progeny of *Malus rockii* which we have classed as pentaploids have less than 85 chromosomes, as is shown in FIG. 12. Olden found counts of 70, 80 and 82 in progeny from open-pollinated *M. sieboldii*. He also found variable chromosome numbers in some segregates as Hewood and Hough (1958) have found in the 'Winter Pearmain' apple and its segregates. As a rule, however, the facultatively apomictic tetraploid apple species usually produce tetraploid or diploid egg cells.

The dominance of facultative apomixis in the polyploid *Malus* species is in accord with the inheritance of facultative apomixis in other polyploid genera (Stebbins 1950). This dominance should facilitate the production of facultatively apomictic hybrid segregates which could be propagated from seed.

## SUMMARY

Facultatively apomictic species of *Malus* include *M. sikkimensis*, *M. rockii*, *M. hupehensis*, *M. toringoides*, *Malus sargentii* and its var. *rosea*. All are polyploids: the tetraploid species produce maternal tetraploids and hybrid triploids or pentaploids; the triploid species produce maternal triploids and hybrid tetraploids; both tetraploids and triploids also produce some aneuploids near the diploid level. Facultative apomixis is a dominant trait in the  $F_1$  hybrids between the facultatively apomictic polyploids and sexual diploids.



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STUDIES IN ARTOCARPUS AND ALLIED GENERA, III.  
A REVISION OF ARTOCARPUS SUBGENUS ARTOCARPUS \*

FRANCES M. JARRETT

Section **Artocarpus**

*Folia* adulta et juvenilia simplicia, integra vel pinnatifida; hypodermis absens vel perfecta, cellis isodiametricis composita, rariter imperfecta (*A. blancoi*). *Inflorescentiae* bracteis interfloralibus sparsis vel absentibus. *Capitula mascula* cylindrica vel clavata, rariter ellipsoidea. *Syncarpia* cylindrica vel ellipsoidea, rariter subglobosa, processibus carnosus, firmis vel flexuosis oblecta, vel areolata; ovaria stylis lateralibus vel sub-basalibus; semina testis, pericarpis, perianthisque variis inclusa; embryum oblique positum, cotyledonibus aequalibus vel inaequalibus, radícula ventrali.

The classification of this section is discussed in detail above (p. 130). The definition given here does not take into account the characters of the anomalous species.

Series **Incisifolii** Jarrett, ser. nov.

*Folia* adulta et juvenilia simplicia, integra vel pinnatifida; hypodermis absens vel rariter imperfecta (*A. blancoi*); glandulae immersae, capitibus planis, 8(-16)-cellis. *Inflorescentiae* ramulis latae. *Capitula mascula* superficie plana. floribus fertilibus vel aliquibus sterilis, solidis praelongisque oblecta, bracteis sparsis vel absentibus. *Syncarpia* processibus saepe ex pilis inflatis asperis, aequalibus vel nonnullis solidis praelongisque oblecta; bracteis sparsis vel absentibus; semina testis tenuiter pergamentaceis, rubris vel brunneis, pericarpis induratis perianthis tenuisque inclusa.

The rather thick, yellowish, completely indurated pericarp and the relatively well-developed radicle of the embryo are characteristic of this series.

The species of this series are somewhat difficult to define, especially in respect to the vegetative characters and the size of the male heads, but they can readily be identified when bearing syncarps. In all the species pinnatifid leaves may occur on the adult tree, so far as can be judged from the collections seen, whereas such leaves are a juvenile characteristic in the rest of the genus. The indumentum of the leaves and twigs is very variable in both quantity and type. However, the hairs can be classified as follows: short, whitish (if abundant, appearing greyish), rough-walled hairs; short, whitish, smooth-walled hairs with uncinat tips; longer, rufous to

\* Continued from volume XL, p. 155.

whitish, smooth-walled hairs. The uncinat hairs are patent, but the other types may be appressed or patent, and straight or somewhat undulate. Some intergrades occur, but the indumentum can usually be described in terms of these three types of hairs, all of which may occasionally (in *A. communis*) occur on the same leaf. The inflated hairs found on the inflorescences, except in *A. communis*, are characteristic of the series.

In considering the species of this series, *Artocarpus pinnatisectus* and *A. multifidus*, both from the Philippines, can first be distinguished from the rest by their deeply pinnatifid, many-lobed leaves, their large anthers 1.2–1.5 mm. long, and the occurrence of elongate, solid, sterile perianths at least in the male inflorescences. The newly described *Artocarpus multifidus* is a very well marked species, although it is based on only two collections, male and female respectively. The inflorescences of both sexes have numerous elongate, solid perianths (projecting 2 mm. in the male head and 15 mm. in the syncarp) with inflated, strongly recurved hairs, and the leaves have seven to ten pairs of lateral lobes. *Artocarpus pinnatisectus* is based on equally limited material, and is not so well defined as a species. In both the collections examined the leaves have twelve to twenty pairs of lateral lobes. The male heads on one of the collections have slightly elongate sterile flowers (projecting only c. 0.5 mm.). The syncarp on the other has no solid processes but in its dimensions ( $15 \times 5$  cm., submature), and in the size of the processes ( $3 \times 2$  mm.), as well as in the simple styles, it differs from the other Philippine species of the series. While these inflorescences are referred to the same species primarily on the basis of the shape of the associated leaves, their characters are not incompatible with each other and each can be distinguished from all the other species of the series. It should be noted that the absence of a hypodermis in the leaves, the shape of the gland-hairs, the inflated hairs on the syncarp, and also the characters of the embryo and pericarp in *A. multifidus*, justify the placing of these species in series *Incisifolii*, in spite of the differences between them and the other members of the group.

In the remaining species the leaves have not more than five (rarely up to nine) pairs of lateral lobes with shallower sinuses, and only in *Artocarpus communis* are the adult leaves typically incised. In *Artocarpus blancoi*, *A. treculianus* and *A. horridus* the leaves apparently become entire on the mature tree, at least on the smaller twigs. In these four species the anthers are shorter, 0.3–0.8 mm. long, and all the flowers are fertile. In spite of the great variability of *Artocarpus communis*, especially under cultivation, this species is distinguished from the three others by the larger inflorescences, the slender processes on the syncarp, varying to low facets or mere areolae, and the absence of inflated hairs. *Artocarpus horridus*, a new species from the Moluccas, is distinguished primarily by the remarkable, pungent, rufous hairs on the twigs, stipules, petioles and peduncles, but also by the syncarp, which blackens on drying and usually appears cinereous with inflated hairs covering the short-cylindric processes ( $3 \times 1.5$ –3 mm.). In the Philippine species these hairs are yellow to brown, and the syncarp is not usually nigrescent. The two other species in the

series, *Artocarpus blancoi* and *A. treculianus*, are from the Philippines. Although closely allied to each other, they differ consistently in the characters of the syncarp; the processes in the former are flexuous, projecting 8 to 15 mm., but in the latter they are short-cylindric, projecting to only 4 mm. There also appears to be a difference in the orientation of the embryo, but insufficient material has been examined for this to be certain. The male head in *A. treculianus* is more slender (c. 7 mm. thick instead of 13–20 mm.), and the anthers are shorter (0.3–0.5 mm. instead of 0.8 mm.). The vegetative characters of the two species overlap, but *Artocarpus blancoi* tends to have larger, more pubescent leaves; specimens with small, entire, subglabrous, rhomboid leaves may be assigned with certainty to *A. treculianus*. The two species overlap in their distribution only in central Luzon, and otherwise they occur in areas with a slightly different climate.

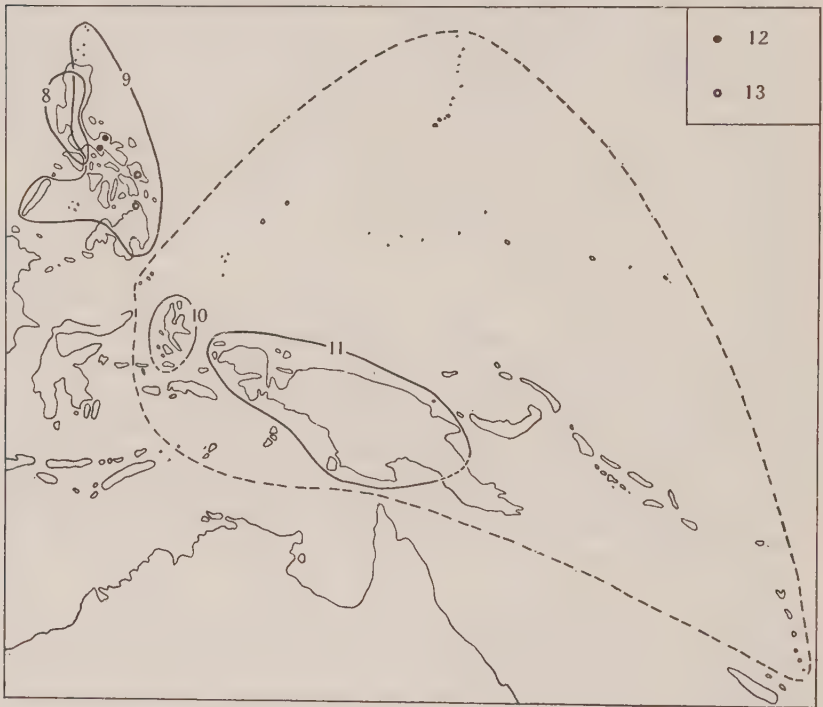


FIG. 12. Distribution of the species of series INCISIFOLII. 8, *Artocarpus blancoi*; 9, *A. treculianus*; 10, *A. horridus*; 11, *A. communis*, distribution as a wild plant — probably indigenous within the area enclosed by the solid line and perhaps also within some part of the region enclosed by the broken line; 12, *A. pinnatisectus*; 13, *A. multifidus*.

There are a few collections referable to this series from the Philippines (all with male inflorescences) which are intermediate in their characters between the species as here defined. It is suggested that these are of hybrid



origin, with *Artocarpus treculianus* as one of the parents; they are described and discussed under that species.

8. *Artocarpus blancoi* (Elmer) Merr. Enum. Philip. Pl. 2: 40. 1923; Quis. Med. Pl. Philip. Is. 226. 1951.

*Artocarpus communis blancoi* Elmer, Leaf. Philip. Bot. 2: 617. 1909. Holotype, Lamao River, Mt. Mariveles, Bataan Prov., Luzon, *Bordeni* 488 (FB 1682), Aug. 1904 (PNH, destroyed, no duplicate seen); neotype, Luzon, *Ramos* BS 42018 (K).

*Artocarpus communis* Forst. var., Merr. Sp. Blancoanae, 124. 1918.

*Artocarpus incisa* Linn. f. var. *blancoi* Elmer ex Merr. Enum. Philip. Pl. 2: 40. 1923, pro syn., sphalm.

*Artocarpus incisus* auct. non Linn. f., Blanco, Fl. Filip. 668. 1837, ed. 2. 465. 1845, ed. 3. 3: 75. 1879.

*Artocarpus communis* auct. non Forst., Merr. Philip. Jour. Sci. 1, Suppl. 43. 1906.

Evergreen trees, height to 15 m. *Twigs* 9–22 mm. thick, shallowly rugose, greyish pubescent, hairs patent or appressed, usually also villous below stipular scars with longer (to 3 mm.), patent, greyish or pale rufous hairs; annulate stipular scars 1 mm. broad, prominent, conspicuous; lenticels scattered. *Stipules* 7–21 cm. long, broadly lanceolate, acute, villous with patent greyish or pale rufous hairs to 3 mm. long, varying appressed-pubescent. *Leaves* c. 20–60 × 20–40 cm., ovate-elliptic, acute, base cuneate or rounded, entire or pinnatifid, lateral lobes 1–3 pairs, broad, acute, sinuses fairly broad, extending halfway to the midrib; main veins prominent beneath, intercostals slightly so; glabrous above except for scattered hairs on main veins, greyish subappressed-pubescent throughout beneath, the hairs rough-walled, straight or slightly undulate, often with longer, greyish, patent, smooth-walled hairs on the main veins; lateral veins c. 12 pairs, straight; intercostals parallel; drying pale brown or greenish, varying dark brown; hypodermis sometimes present, irregular, interrupted, the cells isodiametric in surface view; gland-hairs immersed, heads flattened, 8-celled; petiole 35–130 mm. long.

*Inflorescences* solitary in leaf-axils. *At anthesis: male head* 100–210 × 12–20 mm., cylindric, smooth, covered by flowers, with or without occasional bracts; perianths tubular, 2 mm. long, bilobed above, the lobes with deflexed, inflated hairs having acute tips; stamen 2.7 mm. long, filament fairly slender, cylindric, anther-cells oblong, 0.7 mm. long; bracts slenderly stalked, heads spathulate, to 0.2 mm. across, pubescent (appearing as tufts of hairs on the surface); peduncle 17–37 × 3 mm., greyish or pale rufous villous, varying appressed-pubescent; *female head* with bifid styles exerted to c. 1 mm. *Syncarp* to 10 × 6.5 cm., ellipsoid, drying yellow-brown to brown, covered by closely set, flexuous, tapering obtuse processes, 8–15 × 1.5 mm., rough from the acute, deflexed tips of dense, inflated hairs; scattered bracts usually present between the processes, slenderly stalked, heads narrowly peltate, to 0.2 mm. across, pubescent; wall c. 2 mm.

thick; fruiting perianths numerous, proximal free region thin, not fleshy, "seeds" (pericarps) ellipsoid,  $12 \times 9$  mm., style sub-basal, testa thinly pergamentaceous, embryo with the radicle ventral, the cotyledons parallel to the median plane of the ovary, equal; core c. 10 mm. across; peduncle  $35-60 \times 5$  mm., indumentum as male.

VERNACULAR NAMES: *Antipolo* or *Tipolo* (Tagalog, Bisayan).

DISTRIBUTION: in lowland forest, in areas with a rainfall of at least 80 inches but a distinct dry season, Mindoro, Luzon.

Philippine Islands. MINDORO. Pinamalayan, *Merrill 2138* (NY, US, ♂). LUZON. Abra: Dolores, *Fenix BS 26714* (US, ♂). Ilocos Sur: *Paraíso FB 25825* (A, US, ♀). Isabela: Ilagan, *Vidal 3847* (K, ♂). Zambales: *Curran FB 5805* (US, ♂). Bataan: Mariveles, *Ahern 787* (US, ♂); Mt. Mariveles, Lamao River, *Barnes FB 527* (K, NY, US), *Borden FB 1297* (NY, US), *1380* (US), *Curran FB 7514* (NY), *Williams 360* (K, NY, US, ♂). Bulacan: Angat, *Ramos & Edano BS 34204* (GH). Rizal: Antipolo, *Merrill SB 214* (A, BO, GH, L, NY, P, US, ♀), *Ramos 1819* (BM, BO, GH, L, P, SING, ♂), *Ramos BS 42018* (A, BO, K, L, SING, US, ♀); San Mateo, *Vidal 1547* (A, K, L, ♀). Laguna: Copeland Height, College of Agriculture, Los Banos, *Sulit PNH 15695* (PNH, ♀). Cultivated. LUZON. Manila, Hort. Bot., *Loher 5018* (K, US, ♀).

This species has been identified from Elmer's description and from the two collections cited by Merrill (1923) in raising the variety to specific rank (*Merrill SB 214* and *Ramos 1819*). Merrill (l.c.) stated that *Artocarpus blancoi* also occurred in Palawan, the Batanes Islands, Negros and Mindanao, but he may have been misled by the earlier confusion between it and *A. communis*. In his paper "The Flora of the Lamao Forest Reserve" (1906) he listed several collections under the name *A. communis*, but those which have been seen are all here referred to *A. blancoi* (*Borden FB 1531, 1544, 1624, 1682* are unaccounted for; the last is the type of *A. blancoi*). Other references to *A. communis* as occurring wild in the Philippines are discussed under that species.

The names *Antipolo* and *Tugup* seem to belong to *Artocarpus blancoi* and *A. treculianus* respectively, but they are not always strictly applied. They first appear (the former as *Atipolo*) in G. J. Kamel's account of the flora of the Philippines (Ray, Hist. Pl. 3, App. 52. 1704) and the descriptions there do not conflict with this usage, although they are not sufficiently precise for accurate identification of the species intended.

9. *Artocarpus treculianus* Elmer, Leaf. Philip. Bot. 2: 617. 1909, "*tréculiana*"; Merr. Enum. Philip. Pl. 2: 43. 1923. Holotype, Negros, *Elmer 10406* (PNH, destroyed); isotypes (A, BM, BO, L); lectotype (BM).

*Artocarpus nigrescens* Elmer, Leaf. Philip. Bot. 2: 614. 1909; Merr. Enum. Philip. Pl. 2: 42. 1923. Holotype, Negros, *Elmer 9795* (PNH, destroyed); isotypes (A, BM, BO, L); lectotype (BM).

*Artocarpus ovatifolia* Merr. Philip. Jour. Sci. Bot. 9: 268. 1914, Enum. Philip. Pl. 2: 42. 1923. Holotype, Luzon, *Ramos BS 15040* (PNH, destroyed); isotype and lectotype (BM).

*Artocarpus ovatifolia* Merr. var. *dolichostachys* Merr. Enum. Philip. Pl. 2: 43. 1923. Holotype, Samar, *Ramos* 1603 (PNH, destroyed); isotypes (BM, BO, GH, L, P, SING); lectotype (BM).

*Artocarpus sorsogonensis* Elmer ex Merr. Enum. Philip. Pl. 2: 42. 1923, et Elmer, Leaflet. Philip. Bot. 10: 3807. 1939, pro syn.

*Artocarpus communis* auct. non Forster, Merr. Philip. Jour. Sci. Bot. 3: 401. 1908.

Evergreen trees, height to 20 m. (–40 m., fide Merrill, 1914), with small buttresses, bark grey. *Twigs* 4–12 (–20) mm. thick, shallowly rugose, appressed-puberulent, rarely shortly appressed-pubescent and sparsely villous below the stipular scars with patent, pale rufous hairs; annulate stipular scars c. 1 mm. broad, slightly prominent, conspicuous; lenticels scattered. *Stipules* 5–18 cm. long, lanceolate, acute, cinereous with minute appressed hairs, varying greyish appressed-pubescent. *Leaves* 13–35 (–40)  $\times$  5–25 (–30) cm., ovate, elliptic or rhomboid, acute or short-acuminate, base cuneate or rounded, entire or pinnatifid, lateral lobes 1–3 pairs, narrow, lanceolate, attenuate, sinuses extending up to two-thirds the distance to the midrib, wide or narrow; main veins prominent beneath, intercostals less so, reticulum scarcely prominent; glabrous above, the main veins only appressed-puberulent beneath, varying to shortly greyish subappressed-pubescent throughout, the hairs rough-walled, straight or slightly undulate; lateral veins 9–12 pairs, straight; intercostals parallel; dark green and glossy above, paler beneath, drying yellow-green to dark brown, usually paler beneath; hypodermis absent; glands sunken, heads flattened, 8-celled; petiole (20–)30–80 mm. long.

*Inflorescences* solitary in leaf-axils. *At anthesis: male head* 10–210  $\times$  c. 7 mm., cylindric, smooth, covered by flowers; perianths tubular, 1–1.8 mm. long, shortly bilobed above, lobes with deflexed, inflated hairs having acute tips; stamen 1.5–2.3 mm. long, filament slender, cylindric, anther-cells oblong, 0.3–0.5 mm. long; peduncle 12–27  $\times$  1–2 mm., appressed-puberulent; *female head* with bifid styles exerted to c. 1 mm. *Syncarp* to 7  $\times$  5 cm. (*Ramos & Pascasio* BS 34736, 11  $\times$  3 cm.; fide *Elmer* 9795 to 10  $\times$  7.5 cm.), ellipsoid to cylindric, yellow, drying yellow-brown to brown, covered by closely set, fleshy, cylindric, obtuse processes c. 4  $\times$  2.5 mm., rough from the acute, deflexed tips of inflated hairs; wall c. 2 mm. thick; fruiting perianths numerous, proximal free region thin, not fleshy, “seeds” (pericarps) ellipsoid, 12  $\times$  7 mm., style sub-basal, testa thinly pergamentaceous, embryo with the radicle ventral, the cotyledons transverse to the median plane of the ovary and horizontal or nearly so, the upper one smaller; core c. 10 mm. across; peduncle 20–50  $\times$  2.5 mm., appressed-puberulent.

VERNACULAR NAMES: *Tugup*, *Togop* and variants (Bisayan). Uses: the timber is valuable.

DISTRIBUTION: in forest to 2500 ft. in regions with a rainfall of at least 60 inches and the dry season short or absent, Philippine Islands.

Philippine Islands. PALAWAN. Puerto Princesa, Mt. Pulgar, *Elmer* 13135 (A, BM, BO, GH, L, U, US, ♀). BATANES ISLANDS. *Fenix* BS 3613 (US, ♀). BABUYAN



ISLANDS. Camiguin Island, *Fenix BS 4069* (US, ♀). LUZON. Cagayan: Mt. Tabuan, Bauan, *Ramos BS 77064* (SING, ♀). Isabela: *Alvarez FB 18566* (US, ♂); San Mariano, *Ramos & Edano BS 46941* (BM, NY, ♀). Quezon (Tayabas): Baler, Cemento River, *Quisumbing PNH 2508* (A, PNH, SING, ♀); Casiguran, *Ramos & Edano BS 45408* (A, BM, BO, K, P, US, ♂, ♀); Pagbilao, *Merrill 2848* (BM, NY, P, US, ♀). Laguna: *Ramos 1390* (A, BO, L, P, SING, ♂); San Antonio, *Ramos BS 15040*, June 1912 (BM, ♀), *20530* (K, US, ♀). Camarines: *Alvarez FB 21424* (BM, K, L, P, ♀), *21438* (BM, K, P, ♀), *Vidal 3843* (K, ♀). Sorsogon: *Vidal 3842* (A, K, ♂, ♀); Irosin, Mt. Bulusan, *Elmer 15785* (A, BM, BO, C, GH, K, L, NY, P, U, US, ♀). SIBUYAN. Magellanes, Mt. Giting-Giting, *Elmer 12468* (A, BM, BO, K, L, ♀). TICA0. *Clark FB 1081* (K, NY). SAMAR. *Ramos 1603*, Apr. 1914 (BM, BO, GH, L, P, SING, ♂). LEYTE. Palo, *Elmer 7097* (A, BO, K, ♂). NEGROS. Oriental, Dumaguete, Cuernos Mts., *Elmer 9795*, Apr. 1908 (A, BM, BO, L, ♀), *10406*, June 1908 (A, BM, BO, L, ♀). PANAY. Iloilo, Miagao, *Vidal 3835* (K, ♀). GUIMARAS. *Gammill 310* (NY, US, ♀), *865* (BM, US). MINDANAO. Surigao: *Ramos & Pascasio BS 34736* (A, US, ♀). Davao: *De Mesa FB 27624* (K, US); Todaya, Mt. Apo, *Elmer 10931* (A, BM, BO, K, L, ♀). Bukidnon: near Tanculan, *Fenix BS 24969* (A, P, ♀). Cultivated. OKINAWA. Naha, near Yogi Agricultural Institute, *Walker, Tawada & Amana 6051* (A, ♀).

Three specific names based on this species have been published. Of the two species simultaneously described by Elmer (1909), *Artocarpus treculianus* was based on a specimen with entire, pubescent leaves, while *A. nigrescens* was described from a specimen with incised, subglabrous leaves. The type of the third species, *A. ovatifolia* Merrill (1914), has entire, subglabrous leaves. The name of Elmer's second species was derived from his description of the fruits as blackening on the tree. However, these may have been decayed, since all three types have mature or submature syncarps and in the other two descriptions the fruits are stated to be yellow. This is supported by the only field note available, on *Walker et al. 6051*, "fruits yellowish, fleshy, falling before ripe." Therefore, since *A. nigrescens* was based on an erroneous character, *A. treculianus* is here chosen as the name for the species. (Although it is rather surprising that *A. treculianus* should have been introduced to Okinawa, the vegetative characters of the collection cited above are in agreement and the fruit undoubtedly belongs to this species.)

In addition to the characters of the syncarp, this species is distinguished by the consistently slender male heads, but although these have a nearly constant thickness, their length is very variable. The two collections with male inflorescences seen from mid-Luzon (Quezon and Laguna Provinces) have heads 1 to 2.5 cm. long, while the three seen from farther south (Sorsogon Province, Luzon, Samar and Leyte) have heads ranging from 13 to 21 cm. in length. The latter form was distinguished by Merrill as *A. ovatifolia* var. *dolichostachys*, based on *Ramos 1603* from Samar. He had described *A. ovatifolia* from a female collection, *Ramos BS 15040*, but since this came from Laguna Province, Luzon, the distinction is in accord with the limited evidence, which indicates that the variation has a geographical basis. *Artocarpus treculianus*, on the other hand, was described from Negros and presumably represents Merrill's long-headed va-



riety, so that, if the short-headed form were to be regarded as representing a distinct infraspecific taxon, a new name would be needed. However, since only two collections have been seen with the short male head and there is no other distinguishing character, they are not here separated, although future collecting may show that this would be justified.

The majority of the fertile material from the Philippines which is referable to series *Incisifolii* can be assigned readily to one of the species here recognized, but there are a few anomalous collections, all with subglabrous leaves and male inflorescences. These are described briefly below.

*Ramos & Edano BS 49334*, Mati, Davao Province, Mindanao (SING, ♂): leaves (detached) pinnatifid, lobes 2 or 3 pairs, sinuses extending halfway to the midrib, subglabrous; male head (detached, at anthesis)  $115-145 \times 9-12$  mm., anther-cells 0.8 mm. long, bracts absent, peduncle  $25-35 \times 2$  mm., appressed-puberulent. *Fox PNH 9171*, Karlagen, Pollilo Island (PNH, ♂); twigs and stipules appressed-puberulent; leaves entire, subglabrous; male head (nearly at anthesis)  $65 \times 12$  mm., anther-cells 0.6 mm. long, bracts absent, peduncle  $20 \times 2$  mm., appressed-puberulent. *Curran FB 10164*, Laguna, Luzon (us, ♂): twigs subglabrous; stipules appressed-puberulent; leaves entire, subglabrous; male head (immature) to  $40 \times 8$  mm., a few solid, sterile perianths projecting 0.3 mm. from the surface, anther-cells 0.6 mm. long, bracts scattered, heads spatulate, peduncle  $15 \times 1$  mm., appressed-puberulent. *Curran 3807*, Palawan (BO, K, ♂): twigs and stipules shortly appressed-pubescent, sparsely villous from patent, pale rufous hairs; leaves pinnatifid, lobes 1-2 pairs, sinuses extending one-third the distance to the midrib; male head (immature)  $50 \times 9$  mm., numerous solid, sterile perianths projecting 0.3 mm. from the surface, anthers 0.8 mm. long, bracts scattered, heads spatulate, peduncle  $10 \times 2$  mm., indumentum as twigs.

All four collections could be referred to *A. treculianus* on their vegetative characters, especially the glabrous leaves, but the male heads are too stout, being intermediate in size to *A. blancoi*, and the anthers are too large, agreeing better with the latter species. The last two collections differ from both these species in having sterile flowers, as well as interfloral bracts. They cannot be assigned to *A. pinnatisectus* or *A. multifidus*, however, because of the small anthers (which in these species measure 1.2-1.5 mm.) and, on present evidence, because of the shape of the leaves. It is suggested that these collections are from trees of hybrid origin and that the characters of the first two can be accounted for if they represent *A. treculianus*  $\times$  *A. communis*. The difference in the size of the male heads would correspond to the variation in *A. treculianus*. The second two collections could represent hybrids of *A. pinnatisectus*, perhaps also with *A. treculianus*, although the former species has not been collected in Palawan. In *Curran FB 10164* the pollen grains are shrunken, but they are apparently well formed in the first two collections. However, although this is one explanation of the characters of these collections, basing the parentage partly on geographical evidence, the first two collections, at least, may represent merely a wider range of variation in *A. treculianus* than is here recognized.

10. *Artocarpus horridus* Jarrett, sp. nov. Holotype, Halmaheira, *Beguín* 1976 (L); isotypes (BO, L).

*Soccus silvestris* Rumphius, Herb. Amb. 1: 114. t. 34. 1741.

*Artocarpus communis* Forster var. *pungens* J. J. Smith ex Heyne, Nutt. Pl. Ned. Ind. ed. 2. 1: 557. 1927, non *Artocarpus pungens* (Lesquereux) Hollick, Geol. Surv. Louisiana Spec. Rep. 5: 281. t. 38, figs. 1, 2. 1899.

*Artocarpus elasticus* auct. non Reinw. ex Blume, Hassk. Abh. Naturf. Ges. Halle 9: 158. 1866; Merr. Interpr. Rumph. Herb. Amb. 191. 1917.

*Syncarpia cylindrica*, ad  $9 \times 4.5$  cm., processibus crebris, brevibus, cylindricis, obtusis, canis ex pilis inflatis, vel glabris oblecta; folia integra vel pinnatifida, glandulis immersis, capitibus planis, 8-cellis; ramuli, stipulae, petioli, pedunculique horridi, pilis patentibus, rigidis, aciculiformibus, rufis, 2 mm. longis.

Arbores ad 35 [–40] m. altae. *Ramuli juniores* 12 [6–15] mm. crassi, rugosi, horridi, pilis patentibus, rigidis, aciculiformibus, rufis, 2 mm. longis, numerosis ad paucis, nec non appresse puberulentes; cicatrices stipularum annulatae, 1 mm. latae, prominulae, conspicuae; lenticellae infra cicatrices circum ramulos dispositae. *Stipulae* 9 [6–27] cm. longae, horridae, pilis ut ramulis, appresse pubescentes, pilis canescentibus. *Folia* c.  $30 \times 20$  [20–70  $\times$  10–55] cm., ovati- [vel rhomboido-] elliptica, breviter acuminata, basi rotunda vel cuneata, subintegra, laciniis lateralibus utrinque 3, brevissimis, [integra vel pinnatifida, sinusibus angustis, laciniis utrinque ad 9, lanceolatis, acutis vel breviter acuminatis,] supra saepe appresse puberulentia, costa nervis lateralibus transversalibusque subtus prominentibus, undique appresse pubescentibus, [saepe] horridisque, pilis ut ramulis, venulis subtus prominulis, in sicco rufi-brunnea; nervi laterales utrinque 11–18, recti; nervi transversales paralleli; hypodermis absens; glandulae immersae capitibus planis, 8-cellis; petiolus 45–90 mm. longus.

*Inflorescentiae* axillis foliorum solitariae. *Ad anthesin*: *capitula mascula* c.  $50 \times 15$  [50–95  $\times$  (5–)15–23] mm., cylindrica, plana, floribus numerosissimis oblecta; perianthia tubulosa, 1 mm. longa, supra bilobata, glabra vel pilis paucis, inflatis, apicibus acutis deflexis; stamina 1.6 mm. longa, filamentis cylindricis cellis antherum oblongis, 0.6 mm. longis; pedunculus 20–35 [–50]  $\times$  5 mm., indumento ut ramulis; *capitula feminea* stylis bifidis 2 mm. exsertis. *Syncarpia* 5.5–9  $\times$  3 (–4.5) cm., cylindrica [vel subellipsoidea], flava, in sicco nigrescentia, processibus crebris, solidis, cylindricis, obtusis, 3  $\times$  1.5–3 mm., canis ex pilis inflatis, apicibus acutis, deflexis, vel glabris, oblecta; pedunculus c. 80 [ (–110) ]  $\times$  6 mm., indumento ut ramulis.

VERNACULAR NAMES: *Dinga*, Halmaheira, Ternate; *Pongo*, Halmaheira.

DISTRIBUTION: in evergreen forest to 1000 ft., the Moluccas (Halmaheira group).

MOLUCCAS. MOROTAI. Totodoku, bb 33816, 33817, 33864, (L); W. Pitu, *Beguín* 2223 (BO, L, ♂, ♀). HALMAHEIRA. Djailolo, Togoair, bb 23731 (BO, L); Galela, *Beguín* 1954 (BO, L, ♂, ♀); Galela, Soa Tobara, *Beguín* 1906, (BO, L, ♂), 1908

(BO, L, ♀), 1975, 1976, May 1922 (BO, L, ♂, ♀); Kp. Goal, *Pleyte* 190 (L); W. Tobelo, *Beguín* 2293 (BO, ♀), 2295 (BO, K, L, ♀). TERNATE. Foramadiah, *Beguín* 1233 (BO, L, ♂, ♀). BATJAN. Saoran Domut, *bb* 23200, 23204 (BO, L).

*Artocarpus horridus* is remarkable for the sharp, rigid hairs on the twigs and peduncles, which make specimens unpleasant to handle, and from which the specific epithet is derived. These hairs, combined with the frequently entire leaves and the relatively small syncarp (as compared with *A. communis*), enable the species to be identified with Rumphius' *Soccus silvestris*, or *Socun Utan*, with certainty. J. J. Smith labelled the Beguin collections as *Artocarpus communis* var. *pungens*, but the name was not published until Heyne took it up in 1927. The latter, however, did not provide a description or cite Beguin's collections, but identified the variety correctly with Rumphius' description and plate, so that these must be regarded as the type of Smith's name. Rumphius recorded the species from Amboina and adjacent islands.

The collections seen are rather variable in the shape of the leaves and the inflorescences and in their indumentum, but at least a few rigid hairs are always present. Large, pinnatifid leaves and numerous rigid hairs appear to be correlated with stout inflorescences having dense inflated hairs, while specimens with small, entire leaves and sparse rigid hairs have slender, subglabrous inflorescences. The first type may represent collections made from young trees or juvenile shoots.

11. ***Artocarpus communis*** J. R. & G. Forster, Char. Gen. 101. *t.* 51, 51a. 1776. Holotype, without provenance, *Forster s.n.* (BM); ? isotype, Tahiti (K).

*Camangsi*, *Rhymay Marianorum* et *Dugdug Marianorum* Kamel in Ray, Hist. Pl. 3, App. 52. 1704.

*Soccus lanosus* Rumphius, Herb. Amb. 1: 110. *t.* 32. 1741.

*Soccus granosus* Rumphius, l.c., 112. *t.* 33.

*Sitodium-altile* [Banks & Solander ex] Parkinson, Jour. Voy. Endeavour, 45. 1773, nomen subnudum.

*Rima* Sonnerat, Voy. Nouv. Guin. 99. *t.* 57-60. 1776.

*Rademachia incisa* Thunb. Vet. Akad. Handl. Stockholm 37: 253. 1776; Houttuyn, Nat. Hist. II. Pl. 11: 449. Holotype, Java, *Thunberg s.n.* (UPS, not seen); ? isotype (L).

*Sitodium incisum* Thunb. Philos. Trans. Roy. Soc. London 69: 465. 1779, nomen illegitimum.

*Artocarpus incisus* Linn. f. Suppl. Pl. 411. 1781.

*Artocarpus incisifolia* Stokes, Bot. Mat. Med. 4: 331. 1812, nomen illegitimum.

*Artocarpus nucifera* [Thompson,] Cat. Maurit. 25. 1816, nomen nudum.

*Arctocarpus camansi* Blanco, Fl. Filip. 670. 1837.

*Arcthocarpus rima* Blanco, l.c., 671.

*Artocarpus laevis* Hassk. Flora 25(2), Beibl. 18. 1842. Holotype, Java, Batavia (cult.), *Hasskarl s.n.* (L).

*Artocarpus mariannensis* Tréc. Ann. Sci. Nat. Bot. III. 8: 114. 1847. Holotype, Marianas Islands, *Gaudichaud s.n.* (P).

*Artocarpus incisa* Linn. f. *β laevis* Miq. Fl. Ind. Bat. 1(2): 285. 1859.



*Sitodinium utile* Solander ex Seem. Fl. Viti. 255. 1868, pro syn., errore pro *Sitodinium altile*.

*Artocarpus incisa* Linn. f. var. *muricata* Becc. For. Borneo, 628. 1902. Holotype, New Guinea, *Beccari PP 25* (FI).

*Artocarpus leeuwenii* Diels, Bot. Jahrb. 67: 175. 1935. Holotype, New Guinea, *Docters van Leeuwen 11163* (B, not seen); isotypes (BO, L, U).

*Artocarpus papuana* Diels, l.c., nomen illegitimum, non *A. papuanus* Renner, 1907. Holotype, New Guinea, *Ledermann 7513* (B); <sup>5</sup> isotype (SING).

*Artocarpus altilis* (Parkinson) Fosberg, Jour. Wash. Acad. Sci. 31: 95. 1941, nomen subnudum.

Evergreen or deciduous trees, height to 35 m. *Twigs* 5–15 mm. thick, smooth or rugose, greyish appressed-pubescent, with or without patent rufous hairs below the stipular scars or rarely throughout, varying to glabrous; annulate stipular scars c. 1 mm. broad, slightly prominent; lenticels none or scattered. *Stipules* 10–25 cm. long, lanceolate or broadly lanceolate, greyish or rufous appressed-pubescent, varying to subglabrous. *Leaves* 15–17 × 10–50 cm., rhomboid, varying to elliptic or ovate in outline, base rounded or cuneate, pinnatifid, varying to entire; lateral lobes 1–5(–9) pairs, lanceolate, attenuate, sinuses narrow, extending up to two-thirds the distance to the midrib, varying to deeply pinnatifid with broad sinuses; main veins prominent beneath, intercostals slightly so; puberulent to pubescent on both surfaces with straight, white, usually appressed, rough-walled hairs and/or uncinat, white, patent, smooth-walled hairs, with or without longer rufous (rarely white) appressed, smooth-walled hairs on the main veins, varying to glabrous (seedless cultivars usually subglabrous except on the main veins); lateral veins 9–12 pairs, straight; intercostals parallel; green, usually drying brown to pale brown; hypodermis absent; gland-hairs immersed, heads flattened, 8-celled; petiole 30–60 mm. long.

*Inflorescences* solitary in leaf-axils. *At anthesis: male head* 70–300 (–400) × 15–30(–55) mm., narrowly to broadly cylindric or clavate, rarely ellipsoid, smooth, covered by flowers; perianths tubular, 1–1.5 mm. long, bilobed above, sparsely pubescent or glabrous; stamen 1.6–2.4 mm. long, filament cylindric, anther-cells oblong, 0.6–0.8 mm. long; peduncle 30–60 × 3–6 mm., greyish or rufous villous to glabrous; *female head* with bifid or simple styles exerted up to 2 mm. *Syncarp* (? 10–)15–30 cm. across, cylindric, obovoid, ellipsoid or globose, green to yellow, drying brown to black, covered by closely set, flexuous, attenuate or conical, acute processes, projecting to 15 mm., to 5 mm. across at the base, varying to low facets, or (in seedless cultivars) with the surface merely areolate, pubescent or subhispid with slender patent hairs, varying to glabrous; fruiting perianths numerous, proximal free region thin, not fleshy, “seeds” (pericarps) obovoid-oblong, irregularly compressed, c. 25 × 20 × 15 mm., the style lateral, two-thirds the distance up the ventral face, testa thinly pergametaceous, embryo with the radicle ventral, the cotyledons somewhat oblique to the median plane of the ovary, the lower one slightly larger

<sup>5</sup> It is regretted that the name of the Botanisches Museum, Berlin-Dahlem, Germany, (B), was inadvertently omitted from the list of institutions to which grateful acknowledgement is made for the loan of specimens.



and shallowly folded (cultivars frequently with few or no seeds, the perianths hypertrophied to form starchy edible tissue and the undeveloped ovaries surrounding the core); peduncle  $35-135 \times 5-10$  mm., greyish or rufous villous to glabrous.

VERNACULAR NAMES. (1) General: Breadfruit, restricted to the seedless form in Africa and the New World; Breadnut, seeded form, in the latter regions; Arbre à Pain; etc. (2) Malaysia: *Kulur*, *Kulor* or *Kuror*, seeded, and *Sukun* or *Soccun*, seedless (Malay), Malaysia excluding the Philippines; *Kluwih*, seeded and *Timbul*, seedless (Sundanese), Java; *Camansi*, seeded, and *Rima*, seedless (Tagalog and Bisayan), Philippines; *Gomo*, Moluccas. Only some common forms of the more widely distributed names are given here; Heyne, Nutt. Pl. Indonesië ed. 3. 1: 555. 1950, gives many local names and variants. (3) Pacific: *Dugdug*, seeded, and *Lemai*, seedless, Marianas Islands; *Mai* or *Mei*, Caroline, Marshall, Ellice, Samoa and Marquesas Islands, Niue (e. of Tonga Islands) and Mangareva; *Uto*, Fiji; *Ulu*, Tonga, Samoa and Hawaiian Islands; *Uru* partially replaced by *Maiore*, Society and Austral Islands; *Kuru*, Cook Islands and Mangareva.

USES. The fruit of both the seeded and the seedless forms is an important article of diet in some regions. In New Guinea, Melanesia and the Moluccas the form of chief importance is that with seeds, and these are eaten roasted or boiled. Elsewhere, the seedless form is more commonly cultivated, and in the Pacific it provides the inhabitants of some island groups with a major source of carbohydrate. Different varieties may bear for only a limited period, but a succession of them can provide fresh fruit for most of the year, although the time and length of season, or seasons, varies in the different islands. The fresh fruit is eaten after being cooked by roasting or boiling. The fruit is preserved for the time when it is out of season by being made into a fermented paste which is stored in pits lined with leaves (of *Cordyline* or coconut) and covered with leaves and stones, where it will keep for several months. The paste is called *mar* or *maratan* in the Carolines, *masi* in Samoa and *mahi* in Tahiti. The fruit may also be cut into slices and dried, usually in the sun, for storage. Neither form has become of equal importance elsewhere in the tropics, but the seedless form is widely used as a vegetable, as also is the young fruit of the seeded form in Malaysia. The latex is used in New Guinea and the Pacific for bird-lime and for caulking boats, and the young bark is sometimes used for making *tapa* cloth. The wood is used in the Pacific for building houses and for furniture, but it is of variable quality and is not much valued in other regions.

DISTRIBUTION. Seeded form: probably indigenous in New Guinea, where it is scattered in (?) primary rain forest and is locally abundant in secondary forest on alluvium; perhaps indigenous in Micronesia, where it is a prominent member of the forest on some "high" islands, especially on coralline limestone, and also in Melanesia and the Moluccas; cultivated throughout the tropics (locally naturalized in secondary vegetation, e.g., in Luzon) but rare in Polynesia and generally less frequent than the seed-

less form, except in New Guinea, Melanesia and the Moluccas. Seedless form: cultivated throughout the tropics; many cultivars are distinguished, especially in Polynesia.

**Lesser Sunda Islands.** TANIMBAR ISLANDS. Lurumbun, *bb* 24430, P<sup>6</sup> (L). **Moluccas.** TALAUD ISLANDS. Karakelang, Gunong Duata, *Lam* 2895, P (L). SULA ISLANDS. Kali Waj Gaj, *bb* 28813, P (BO).

**New Guinea.** VOGELKOP. Inanwatan, Tisa, *bb* 32639, P (BO, L); Manokwari, Momi, *Kostermans* 189, P (BO, K, L); Manokwari, Prafi, *NIFS BW* 453 (L, ♂, ♀); Manokwari, Warnapi, *bb* 33667, P (BO); Tangion Bair [= Biak], *Becari PP* 25, Apr. 1872 (FI, ♀); Tanibo, *bb* 25517, P (BO, L). DUTCH NORTH NEW GUINEA. Bernhardt bivak, Idenburg River, *Brass & Versteegh* 13537, P (A, ♀), *bb* 25680, P (BO, L, SING, ♂, ♀); Hollandia, n. of Kobroor, *bb* 25347 (L); Meervlakte, Motorbivak, Bruine River, *Docters van Leeuwen* 11163, R, Nov. 1926 (BO, L, U, ♂, ♀); Pioneerbivak, Mamberamogebiet, *bb* 31100, P, *bb* 31306, P (BO); Prauwenbivak, *Lam* 927 (BO, L, U, ♂, ♀); Sennen, 30 km. inland from Nabire, *Kanehira & Hatusima* 12580, R (A, BO, ♂). DUTCH SOUTH NEW GUINEA. Lorentz River, *Von Römer* 154 (BO, L, ♂, ♀); Mimika, Uta, Aria, *bb* 32858, P (L); Mimika, Uta, Najaja, *bb* 32851, P (L). PAPUA. Central Division: near Port Moresby, *Edelfeldt* 51 (L); Sogeri, *Forbes* 158 (BM, ♀); Veiya, *Carr* 11633, R (A, K, ♀), 11675, S (A, K, ♂). Gulf Division: Vailala River, Lipokira, *Brass* 981, ? cultivated (A, ♂, ♀). Northern Division: Isuarava, *Carr* 15726, S (A, K, ♀). MANDATED TERRITORY OF NEW GUINEA. Morobe District: Markham Valley, Kajabit, *Clemens* 40696 (A, ♂); Sattelberg, *Clemens* 1117 (A, L, ♂, ♀, ? mixed collection). Sepik District: mouth of April River, *Ledermann* 7513, R, June 1912 (B, SING, ♂, ♀). ARU ISLANDS. P. Kobroor, *bb* 25347, P (BO).

The nomenclature of the Breadfruit is discussed in detail above (p. 118) where it is concluded that the correct name is *Artocarpus communis* J. R. & G. Forster (1776). The combination *Artocarpus incisus* (Thunb.) Linn. f. (1781), based on *Rademachia incisa* Thunberg (1776), which was made by Linnaeus *filius* when he chose *Artocarpus* over *Rademachia*, is rejected on the grounds that an earlier legitimate name was available for the species and should have been used. The earliest published Linnaean binomial for the Breadfruit, *Sitodiodium-altile* [Banks & Solander ex] Parkinson (1773)<sup>7</sup> on which *Artocarpus altilis* (Parkinson) Fosberg (1941) is based, is also rejected since the account to which it is attached is considered to be inadequate as a generico-specific description.

*Artocarpus communis* is based solely on the seedless form of the Breadfruit. The type is presumably the Forster specimen in the British Museum (Natural History) consisting of a single incised leaf without provenance.

<sup>6</sup> The following abbreviations are used to indicate the type of forest from which the collection was made: P, old or primary; R, riverside; S, secondary.

<sup>7</sup> A comment may be added here on the hyphenation of the Latin names attached to the series of notes on Tahitian plants in Sydney Parkinson's journal. There is no definite reason for supposing that Stanfield Parkinson added the hyphens in editing his brother's work for publication. On the other hand, the hyphenation by Sydney Parkinson of Solander's manuscript names, in adding them to his notes, is probably an insufficient reason for rejecting the work as one in which binomial nomenclature is not used. The hyphens should be regarded as an orthographic error.

Another specimen collected by Forster, also a single leaf, which is in the herbarium at Kew, was collected on Tahiti, and this may be an isotype. The illustrations in the original account show the male head as narrowly cylindric, the syncarp as subglobose with low facets, and the peduncles of both as sparsely villous. *Sitodium-altile* was likewise based on the seedless Breadfruit of Tahiti. Thunberg's *Rademachia incisa* was described from Java and included both the seedless and seeded forms of the Breadfruit, which he designated as "a.) Pericarpio sterili, muricato, sulcis inter germina reticulato, . . .," and "β.) Pericarpio fertili, germinibus productis & pistillis longis echinato; . . .," respectively. The vegetative characters appear to be taken from the seeded form, since the leaves, petioles and peduncles are described as villous and the seedless form in Java is glabrous or nearly so.

The Breadfruit is cultivated throughout the tropics in both seeded and seedless forms, but in most areas the seedless form is more commonly grown and is of considerably greater importance. A review follows of the variation exhibited by both forms throughout their present ranges, together with a discussion of the ecological status of the former. This survey can be only preliminary, since in most areas insufficient evidence is available concerning the details of variation. A conservative taxonomic treatment is therefore adopted. The aim here is to draw together from a wide geographical area and range of literature the information that is available, and to present the taxonomic problems, thus providing a basis for future, more detailed studies.

Although further studies may show that two or more subspecies or closely allied species are involved, it is tentatively concluded that the Breadfruit, whether seeded or seedless, represents a natural but rather variable species which has been considerably modified under man's influence. The seeded Breadfruit appears to be indigenous in New Guinea and perhaps also in the Moluccas, Melanesia and Micronesia. Some, at least, of the few-seeded or seedless varieties were developed in New Guinea, but others may have arisen from seeded Breadfruit growing in Micronesia, Melanesia and the Moluccas.

In the literature the place of origin of the Breadfruit has been indicated in general terms as the Sunda Islands or Malaysia (e.g., Alphonse de Candolle, Orig. Pl. Cult. 238. 1882), or else as the Pacific (e.g., Burkill, Dict. Econ. Prod. Malay Penin. 250. 1935). It has often not been made clear whether both the seeded and the seedless forms were under consideration, or the latter alone. The fairly consistent and marked differences which exist over wide areas (but not in New Guinea or the Pacific) between the two cultivated forms have led some authors, including Quisumbing (Philip. Jour. Sci. 70: 331. 1940), to suggest that they originated from two distinct wild species. However, as already indicated, a broad view is here taken of *Artocarpus communis*. Moreover, if two or more taxonomic entities should be involved in the ancestry of the Breadfruit, a complex hybridization between them has apparently taken place. It will be shown below that the differences between the seeded and seedless forms



can be accounted for in part by their distribution from different sources.

The distinctions between *Artocarpus communis* and the allied species of series *Incisifolii* are indicated above in discussion of the series. The principal characters in which variation occurs within the species, including cultivars, are the outline and indumentum of the leaves, the shape and size of the male head, the shape, size and surface of the syncarp, and whether or not seeds are formed. Before proceeding with a description of the Breadfruit by geographical areas, the possible causes and consequences of the development of sterility will be discussed.

First, however, it must be pointed out how very inadequate the herbarium material — most of which is sterile — has been as a basis for this survey. For comparative studies over a wide area, material which gives as full a picture as possible of trees representing different variants of the seeded and seedless forms would be of very great interest. The difficulty of making successive collections from a single tree is recognized, but ideally the following material would be necessary: (1) one or more leaves attached to a twig (having a terminal bud enclosed by stipules), with notes on the variation in leaf-shape on different parts of the tree; (2) two or three male inflorescences at anthesis to show the range of variation in shape; (3) a female inflorescence at anthesis; (4) a longitudinal slice of the mature fruit dried rapidly to prevent decay (showing outline, surface, and whether or not seeds are present); (5) drawings or, preferably, photographs to show the habit of the tree and the shape and arrangement of the fruit; and (6) notes on the colour and uses of the fruit and wood, the mode of propagation, vernacular names, etc. If collections can be made only at the time of anthesis, both male and female inflorescences should be gathered. In order to carry out more detailed studies and to establish the cause of the failure to form seeds, field and experimental work in the tropics will be necessary. I am glad to learn from Dr. F. R. Fosberg, Pacific Vegetation Project, National Research Council, Washington, D.C., that such a survey may be carried out in the Pacific region.

The presence or absence of seeds must be treated independently from other variation in the species, and the possible genetic basis and consequences of the sterility considered. Correlations existing between the seeded or seedless character and other variation will be indicated below. The evidence available from the literature shows that triploidy occurs in the seedless form. Chromosome numbers equivalent to a diploid number of 56 have been recorded in *Artocarpus heterophyllus* (Subba Rao, Half-Yearly Jour. Mysore Univ. Sect. B. Sci. 1: 63. 1940; Janaki-Ammal in Darlington & Wylie, Chromosome Atlas ed. 2, 184. 1955), *A. lakoocha* (Banerji & Hakim, Proc. Ind. Acad. Sci. B. 38: 128. 1954) and seeded *A. communis* (Nishiyama & Kondo, Seiken Zihô 1: 26. 1942, reference not seen; Janaki-Ammal in Darlington & Janaki-Ammal, Chromosome Atlas, 184. 1945). A somatic chromosome number of c. 81 has been recorded for seedless *Artocarpus communis* (Nishiyama & Kondo, l.c.). These counts suggest that the basic number for *Artocarpus* is 28 and that the seedless Breadfruit is triploid ( $3n = 84$ ), at least in the example under study. As a genus,



*Artocarpus* appears to be tetraploid with respect to the basic number of 14 that occurs widely in the Urticales. Darlington and Wylie gave the basic number of *Artocarpus* as 14, but their data were derived in part from Krause's study of chromosome numbers in the Moraceae (Planta 13: 29. 1931), and unfortunately the only species studied by the latter was *A. cannonii* W. Bull ( $2n = 28$ ), which had been transferred correctly to *Ficus* by N. E. Brown in 1888. Thus there is as yet no evidence that the diploid number of 28 occurs in *Artocarpus*.

Further investigation will be required to determine whether or not triploidy is the primary cause of the failure to form seeds. The simple occurrence of triploidy would not necessarily result in the formation of a fleshy, edible fruit and it is more likely to have been a secondary development as, for example, in the banana. Some fruits with very few seeds have been seen on collections from New Guinea (e.g., Carr 11633), and in Tahiti and Java varieties are recorded with fruits which are eaten for their flesh but which usually have a few seeds. This tendency to develop only a few seeds may well be due to genetic factors other than polyploidy. Both of the latter varieties are propagated by vegetative means, and Heyne (Nutt. Pl. Indonesië ed. 3. 555. 1950) states that the seeds are not viable in the Javan variety. If triploidy were to arise in such a variety it might be expected to produce more complete sterility and, other things being equal, the triploid plant would presumably tend to be selected.

The seedless varieties of the Breadfruit are most commonly propagated by means of root cuttings and root suckers and the formation of the latter is stimulated by deliberate injury of the roots. Each variety is thus a clone within which the primary source of variation is presumably somatic mutation. This will be the chief means by which new varieties can arise in areas where the seeded form is rare or absent, and that such mutations do occur is evident from comments given with lists of varieties from the Pacific. As suggested by Fosberg (Botanical Report on Micronesia. U. S. Commercial Company Economic Survey of Micronesia. 1946), back-crossing may occur between the seedless and seeded forms of the Breadfruit. If fertile pollen is produced by a seedless variety it may fertilize a seeded variety and carry over characters of the former, including those that have arisen by somatic mutation, thus adding to the general pool of variability in the seeded form. If a genetically determined inability to produce seeds is also transmitted, a new seedless variety may be formed that combines characters of both the seedless and the seeded parents. A triploid seedless variety might be expected to produce occasional haploid and diploid grains which could result in diploid and triploid progeny (the latter, at least, seedless) on successful pollination of the seeded form. Conversely, though less frequently, diploid and triploid (and presumably also tetraploid) progeny might be grown from occasional seeds formed in a usually seedless variety.

The range of variation exhibited by seedless varieties must depend primarily on that of the seeded plants from which they have arisen. The variation observed indicates that only autotriploidy has occurred, if the broad view here taken of *Artocarpus communis* is accepted. There is no taxonomic

evidence from the characters observed that hybridization with the allied species here recognized has occurred during the development of the seeded or seedless Breadfruit. In addition, historical evidence, outlined below, makes it unlikely that the Philippine species, at least, could have taken part in any hybridization. However, although no infra-specific taxa are here proposed within *Artocarpus communis*, this does not exclude the possibility that, when more detailed evidence based on a wide range of vegetative and inflorescence characters is available, two or more subspecies, or closely allied species, in the New Guinea and western Pacific regions may be shown to have been involved in the ancestry of the Breadfruit as it is known today. Many varietal names have been proposed for the seedless as opposed to the seeded form of Breadfruit, but such taxa can only be descriptive, since in different areas there is great and overlapping variation in both forms and the origin of the seedless form is probably complex.

The following subdivision of the areas in which the Breadfruit occurs, according to the status and relative importance of the seeded and seedless forms, is given as a basis for the review which follows: (1) area in which the seeded form is predominant, very variable and probably indigenous — New Guinea and perhaps the Moluccas and Melanesia; (2) area in which the seedless form is predominant and very variable — the Pacific; (2a) area in which the seeded form is a conspicuous and possibly indigenous component of the vegetation — Micronesia; (2b) area in which the seeded form is rare — Polynesia; (3) area in which the seeded and seedless forms are rather constant in their characters and distinct from each other — the remainder of the tropics.

In New Guinea the Breadfruit is of widespread occurrence, especially in its seeded form. It was recorded by Miklouho-Maclay (Proc. Linn. Soc. N. S. Wales 10: 348. 1885; as *A. incisa* and *A. integrifolia*) in the Astrolabe Bay area of Northeast New Guinea, both in cultivation and in the forest, and by Warburg for Finschhafen and the Bismarck Archipelago (Bot. Jahrb. 13: 295. 1891). Lauterbach (l.c. 63: 421, 438, 444, 447. 1930) stated that wild Breadfruit occurred in the Astrolabe Bay area both on the hillside in rainforest and in the secondary alluvial forest. On the Ramu River, he recorded it as characteristic of the latter, being found in places in pure stands. In Papua, White (Proc. Roy. Soc. Queensland 24: 23. 1922) noted that the Breadfruit was "common wild or cultivated through the whole of the coastal country," while Lane-Poole (Forest Resources of Papua and New Guinea, 81. 1925) recorded it as one of the more permanent members of the regrowth on cleared land. In the "Results of the Archbold Expeditions," the Breadfruit was recorded from the Fly River region as common on flooded riverbanks and in second growth forest (Rand & Brass, Bull. Am. Mus. Nat. Hist. 77: 366, 376. 1940). It was also recorded from the Meervlakte in Dutch North New Guinea as occurring along waterways and as a marginal constituent of periodically inundated *Timonius*-forest, one of the successional communities of this flood plain (Archbold, Rand & Brass, l.c. 79: 233, 235, 1942). A photograph of this community was published by Van Steenis (in Nieuw Guinea, ed. Klein,

Pt. II. Veg. en Flora, 228. *t.* 2, 1954). Lam had earlier noted its abundance in this region (Fragmenta Papuana, transl. Lily M. Perry. Sargentia 5, 1945), and in his review of the vegetation and flora of the whole of New Guinea (Blumea 1: 120. *map.* 1934) he described the Breadfruit as a locally frequent constituent of the extensive freshwater swamps. Further west, the Breadfruit was recorded as frequent in the inner part of MacCluer Gulf by Engler in the enumeration of plants collected by Naumann on the voyage of the *Gazelle*. (Bot. Jahrb. 7: 451. 1886). However, Rand and Brass have expressed doubt as to whether the Breadfruit is indigenous in New Guinea, and they took its presence in the Fly River area as "an indication of the presence of human population." As they stated, it is indeed difficult to establish its occurrence in undisturbed climax forest. Nevertheless, several collections have been seen which do appear to be from such forest. The best attested of these is Brass & Versteegh 13537, "frequent tree of primary rain-forest, on slope of a ridge, 650 m. alt." There seems to be no conclusive reason for doubting that the Breadfruit is truly indigenous in New Guinea; moreover, the seeded form shows a wider range of variation there than anywhere else. It evidently is capable of competing with other indigenous species, although its presence is admittedly most conspicuous in the secondary forest.

The seeded Breadfruit shows in New Guinea the full range of variation indicated in the description of the species, except, perhaps, in the shape and surface of the syncarp and in the shape of the male head. It may be noted once more how variable the indumentum is in colour, distribution, abundance, and type and length of hair. The collections listed above include all that were seen from New Guinea. Their provenance is indicated and none was stated to be cultivated, except possibly Brass 981, although some of those from secondary or riverside forest, or for which there are no data, may have been planted. With the exception of Carr 11633, 11675, 15726 (secondary or riverside forest) and Clemens 1117 (no data), which will be discussed below, their inflorescences may be described as follows. The syncarps are ellipsoid to cylindric, with slender flexuous processes projecting to 5–15 mm., and the male inflorescences are narrowly cylindric, 20–30 (–37)  $\times$  1.5–2 cm. This appears to be the indigenous form of the Breadfruit in New Guinea. *Artocarpus leeuwenii* and *A. papuana* of Diels both represent this form. The type of *Artocarpus leeuwenii* (Docters van Leeuwen 11163) has a dense indumentum throughout, and the syncarp processes (erroneously called styles) project to 12 mm., whereas the type of *A. papuana* (Ledermann 7513) has less indumentum and the syncarp processes project only 5–7 mm. Intermediate collections have been seen, however. The type of *Artocarpus incisa* Linn. f. var. *muricata* Beccari resembles that of *A. leeuwenii* in the syncarp characters, but has a sparser indumentum.

The four collections which were excepted above show a wider range of variation. The syncarp on Carr 15726 has low, broad, obtuse processes on the surface and a number of apparently well-developed seeds. Carr 11633 has a syncarp covered by conical processes projecting to 3 mm. and has



only one seed. A similar, possibly entirely seedless, syncarp was seen on *Clemens 1117*. This collection is also of interest since on the specimen at the Arnold Arboretum some of the male inflorescences measure only  $11-13 \times 1.5-1.8$  cm. at anthesis, although on that at Leiden there is one measuring  $25 \times 1.6$  cm. A note on the label at Leiden suggests that this may be a mixed collection. *Carr 11675* has a male inflorescence measuring  $15 \times 1.1$  cm., at anthesis, so that there is evidently fairly wide variation in both male and female inflorescences in collections from secondary and riverside forest. It must be pointed out that all the syncarps seen are ellipsoid to cylindric and that none is undoubtedly seedless. Thus the "characteristic" seedless Breadfruit of the Pacific, with a globose head and a nearly smooth surface has not been seen in New Guinea. Too much emphasis should not be placed on this apparent absence since so few syncarps have been seen, and none is definitely from a cultivated plant. Brass (Bull. Am. Mus. Nat. Hist. 111: 97. 1956) notes that the seeded Breadfruit is cultivated on the Cape Vogel Peninsula for its seeds, and Barrau (Subsistence Agriculture in Melanesia. Bishop Mus. Bull. 219: 59. 1958) states that, especially in New Guinea, the seeds are preferred to the flesh, although the latter is also eaten. It is of interest to note that Ochse and Backhuizen van den Brink (Veg. Dutch E. Ind. 489. 1931) record that F. J. F. van Hasselt, a missionary at Manokwari, stated that the Papuans sliced Breadfruit (presumably few-seeded or seedless) and dried it for storage over a period of time. In view of the variability and apparent overlapping of characters, there is no reason why the few-seeded or (?) seedless varieties should not have arisen in New Guinea.

There is no definite evidence as to whether the Breadfruit is indigenous in Melanesia and the Moluccas. In Melanesia, Guillaumin's observation that it is common in the rainforest on Eromanga in the New Hebrides (Jour. Arnold Arb. 13: 106. 1932) is based on a field note, the only one seen from the whole region, on *Kajewski 394* (A, K). This collection has deeply incised leaves with broad sinuses. The inflorescences are at anthesis; the male head is clavate, measuring  $13 \times 2$  cm., and the female head is obovoid with conical processes projecting 1 mm. However, too much significance cannot be attached to this single record of the status of the Breadfruit, since it is possible that the forest was secondary. Daniker (Viert. Naturf. Ges. Zürich 77: Beibl. 19: 125. 1932) recorded the Breadfruit as doubtfully spontaneous on the Loyalty Islands. The only other fertile collection seen from Melanesia is *Mosely s.n.* (BM, K) from the Admiralty Islands, with male heads measuring  $20-26 \times 3$  cm. at anthesis. It may be noted that the single fertile collection seen from New Caledonia, *Balansa 3233* (P), has a seeded fruit with low facets and a clavate male inflorescence  $7 \times 2.3$  cm.

In the Moluccas, the only source of detailed information is Rumphius, who described (c.1660-1680) distinct seeded and seedless forms in the "Herbarium Amboinense." The former, *Soccus granosus*, had narrowly conical processes on the syncarp and more or less pubescent twigs and leaves, while the latter, *Soccus lanosus*, had low facets on the syncarp and



was glabrous. Rumphius recorded that he had been told that the Breadfruit grew wild on Banda. All the collections from the Moluccas cited above are stated to be from either old or primary forest, but all are sterile, and no other fertile collections from these islands have been seen. In their vegetative characters the collections lie within the range of variation shown by those from New Guinea, but none is as densely pubescent as the type of *A. leeuwenii* and most are subglabrous. Both to the east and west of New Guinea, therefore, the range of variation is apparently fairly wide, but whether these forms could have been derived solely from the apparently indigenous Breadfruit of New Guinea cannot be determined until more adequate material is available. This problem will be discussed further below under Micronesia.

In the Pacific region (i.e., Micronesia and Polynesia) the Breadfruit is chiefly of importance in its seedless form and the variation exhibited by this will first be indicated briefly, since more evidence is available concerning this form than the seeded form. A list follows of the more important references which give lists of Breadfruit varieties under their vernacular names. In the ensuing discussion, where only the date is given after an author's name, it refers to a work in this list.

CHRISTIAN, F. W. The Caroline Islands, 386. 1899. [43 varieties (two seeded) on Ponape, with brief notes on the fruits.]

SEEMANN, B. Flora Vitiensis, 255. 1868. [13 varieties (one seeded), with short notes on the fruits and leaves.]

CHRISTOPHERSON, E. Flowering Plants of Samoa. Bishop Mus. Bull. 128: 72. 1935. [30 varieties, with brief notes on the fruits and leaves.]

BENNETT, G. Gatherings of a Naturalist in Australasia, 396. 1860. [24 varieties in Tahiti, with some brief comments.]

HENRY, T. Ancient Tahiti. Bishop Mus. Bull. 48: 39. 1928. [40 varieties listed, with some short notes. The Tahitian legend of the origin of the Breadfruit is also given (p. 423).]

WILDER, G. P. The Breadfruit of Tahiti. Bishop Mus. Bull. 50. 1928. [31 varieties described (one seeded), with photographs of the fruits and leaves. A number of the vernacular names in these three works are the same.]

CHRISTIAN, F. W. Eastern Pacific Islands, 208. 1910. [34 varieties listed from the Marquesas without descriptions.]

WESTER, P. J. Philip. Agr. Rev. 17: 24. 1924. [A compilation of earlier lists incorporating further data from Tahiti and the Marquesas.]

The variation recorded for the seedless form of the Breadfruit in the Pacific covers the full range indicated for the species in the shape, size and surface of the syncarp, and in the outline of the leaves. The latter are usually incised and glabrous or nearly so except on the main veins, but there are a few entire-leaved varieties. These observations are based on the descriptions of Wilder (1928), on the brief notes of other authors, and on rather sparse herbarium material. On the basis of this evidence it has not been possible to distinguish any obvious groups of varieties. With closer study, however, lines of development between different varieties may well prove to be traceable and it may then be possible to determine the routes of distribution. At present it can be noted only that some of the

seedless varieties show quite a close resemblance to the seeded form of New Guinea in their elongate, "prickly" syncarps. They may be contrasted with other varieties having round, nearly smooth fruits, but all gradations and combinations of characters seem to occur between these two extremes. Seeded varieties of the Breadfruit are rare in Polynesia but have been recorded from Fiji (*uto sore*, Seemann, 1868) and Tahiti (*huero*, Wilder, 1928). It was noted above that the second of these is usually propagated by vegetative means. The fruit is globose, with few seeds and low facets, and the leaves are incised and "slightly pubescent."

The Breadfruit was distributed throughout the Pacific before the arrival of Europeans. The earliest description that has been found of it was given by Quiros, who went as the pilot on Medaña's voyage of 1595 through the southern Pacific Ocean and who, after the death of Medaña on Santa Cruz, guided the survivors of the expedition to Manila (Penrose, *Travel and Discovery in the Renaissance 1420-1620*, 165. 1952). Quiros recorded the Breadfruit from the Marquesas, in the east, and Santa Cruz, in the west, in an account of the voyage which he wrote in the form of a letter to De Morga, then governor of the Philippines, and which the latter included in his "Sucesos de las Islas Filipinas," published in 1609. There can be no doubt that the Breadfruit was introduced into Polynesia by man, and it may be noted that this opinion was expressed as early as 1784 by Forster in his little book "Vom Brodbaum."

In Micronesia, on the other hand, it has been stated that the seeded form is an important constituent of the lowland vegetation on some of the "high" islands. In the eastern Caroline Islands the seeded form has been recorded from all the "high" islands. Kanehira listed two seeded varieties from Truk (edible, *mei chon*; not edible [?], *aroyas*; Jour. Dep. Agr. Kyushu Univ. 4: 306. 1935). Glassman noted two seeded varieties in Ponape, which frequently grew without any cultivation (*mai-pa*, *mai-kohleh*, Bishop Mus. Bull. 209: 11. 1952; cf. *pa*, *koli*, Christian, 1899). On Kusaie, Volkens (Bot. Jahrb. 31: 416. 1901) recorded the Breadfruit (not stating whether it was seeded) from lowland forest. He also mentioned that there were seeded varieties on Yap, but apparently regarded them solely as planted in mixed groves of useful and strand trees. Volkens stated that in the Carolines as a whole most of the primary forest had been destroyed, except on very steep slopes, and Glassman also noted that on Ponape most of the vegetation at low elevations was secondary. Although the seeded form is evidently able to maintain itself, as in New Guinea, in secondary vegetation, authentic records of its occurrence in virgin forest in the Carolines are lacking. Seeded varieties are also recorded from "low" islands in this group, namely, Pingelap Atoll (*mei sabarak*, St. John, Pacif. Sci. 2: 109. 1948), and Namonuito and the Hall Islands (Stone, l.c. 13: 89, 90, 100. 1959). These records indicate that seeded as well as seedless varieties must have been distributed by man in this area; Stone notes that the seeds are a favourite article of diet.

In the Marianas, a seeded form of the Breadfruit called *dugdug* was stated by Safford to be very abundant on Guam (Contr. U. S. Natl. Herb.

9: 55, 190. 1905). Dr. F. R. Fosberg, who has studied this form in the field, has been kind enough to send me the manuscript of a paper he has written on the Breadfruit in Micronesia. He also expresses the doubts indicated above as to the status of seeded varieties of the Breadfruit in the Carolines, but he states that in Guam the *dugdug* is dominant in some of the least disturbed original forest, especially in limestone areas. Its characters are somewhat distinctive and Dr. Fosberg describes the leaves as often entire (although very variable in their outline on the same tree) with conspicuous, brown, appressed hairs on the main veins beneath, the male inflorescences as short (to c. 10 cm. long), and the syncarps as more or less short-cylindric with low facets at maturity. This form was described by Trécul as *Artocarpus mariannensis* from a collection made by Gaudichaud, *sine numero*, in the Marianas Islands. The collection probably comes from Guam, which Gaudichaud visited in 1819 with the Freycinet expedition. The type specimen in the Muséum National d'Histoire Naturelle, Paris, has entire leaves, which are glabrous except for appressed colourless or pale rufous hairs on the underside of the main veins, and an immature male inflorescence with a cylindric head measuring  $7 \times 1$  cm.; the vernacular name is given as *doug-doug*. The few fertile collections seen from Guam indicate that the seedless form of the Breadfruit there, called *lemai*, likewise has rather short, stout male inflorescences, but that the leaves are incised.

From this review it is evident that, throughout the Pacific, the Breadfruit exhibits a range of variation, at least in the shape of the syncarp, beyond that seen so far in collections from New Guinea. On the other hand, in the Pacific region the leaves tend to be subglabrous except on the main veins, and no specimens have been seen with such a dense indumentum as the type of *A. leeuwenii*, which may be regarded as representing almost the extreme of variation in this direction of the presumed indigenous form in New Guinea.

Nevertheless, until additional fertile collections are available, especially from New Guinea and the Carolines (none at all has been seen from the latter area), it is felt that the pattern of variation in the Pacific cannot be established with sufficient certainty to justify the separation of the Guam form of the seeded Breadfruit as a distinct subspecies or species. If this should be a distinct indigenous form and if it has hybridized with an introduced form of the Breadfruit in the Micronesian area, as is suggested by Dr. Fosberg, the characters of the Guam form could account for the greater range of variability of the Breadfruit in the Pacific than in New Guinea. However, it has been indicated in the course of this review that there is a considerable scatter of the characters of this form in the western Pacific area and that most of them (entire leaves, rufous hairs, fairly short male inflorescences and low anthocarp apices) also turn up in collections from New Guinea. There is a possibility that the *dugdug* of Guam represents a very early introduction of a rather distinctive type, developed in the Carolines or in New Guinea, which became naturalized and flourished in part due to lack of competition from the relatively small indigenous flora.

It must be pointed out in this connection that the Breadfruit has a large seed with no powers of dormancy. Furthermore, only two other species of the genus extend farther east into New Guinea than the Vogelkop; of these one extends into the Solomon Islands.

Dr. Fosberg discusses and has drawn my attention to the considerable range shown in the Pacific and elsewhere in the minute details of the indumentum of the leaves (even when consisting of only scattered hairs on the main veins), and differences in the hairs may be of great assistance in tracing the alliances of the different varieties.

In spite of the lack of material from the Carolines it seems that this scattered group of islands may have been a centre of differentiation and of distribution for seedless varieties of the Breadfruit. This is also suggested by the distribution of the names for the Breadfruit which is outlined below, and by the wide range of variation in fruit characters indicated by Christian's notes on seedless varieties in Ponape (1899). This range is apparently as wide as that found farther east and includes the characters of the seeded forms of both Guam and New Guinea. To show to what extent Micronesia was a centre of origin for seedless varieties from seeded trees requires further study, both there and in New Guinea.

Two names for the Breadfruit are widespread in the Pacific, as was pointed out by Christian in 1897 (Jour. Polynes. Soc. 6: 127. 1897). Their distribution is northerly and southerly respectively, but they overlap somewhat, especially in eastern Polynesia. The more northerly of the names is *mai* or *mei*, which occurs in the Caroline and Marshall Islands (Christian, l.c. and 1899, and other authors), in Niue, east of the Tonga Islands (Yuncker, The Flora of Niue Island. Bishop Mus. Bull. 178: 46. 1943) and in Samoa, the Marquesas, and Mangareva in the Tuamotu Archipelago (Christian, 1910). It is also found as *lemai* in the Marianas and as *rima* in the Philippines. The southern name appears as *ulu* in Samoa (Christopherson, 1935), as *kuru* in the Cook Islands (Wilder, Flora of Rarotonga. Bishop Mus. Bull. 86: 40. 1931), and as *uru* in Makatea. In the Tuamotu Archipelago *ura* is recorded from Anaa (Brown, Flora of Southeastern Polynesia — III. Dicotyledons. Bishop Mus. Bull. 130: 37. 1935) and *kuru* from Mangareva (Christian, 1910). Wilder (1928) records that in Tahiti the name for the Breadfruit used to be *uru* ("head"), but that it is now *maiore*. In Hawaii the Breadfruit is called *ulu* and MacCaughy (Torreya 17: 37: 1917) states that the plant was probably introduced there from Samoa. In Fiji, the word for Breadfruit is *uto*, meaning "heart," according to Seemann (1868). Two names which are somewhat similar to those of wide distribution in the Pacific are recorded on collections from New Guinea — *momu*, *momoi*, and *mow* from the Vogelkop, and *unu* from Papua. However, in view of the many and various local names that have been noted for the Breadfruit in New Guinea and Melanesia (Christian, Jour. Polynes. Soc. 6: 128. 1897; Barrau, Jour. Agr. Trop. Bot. Appl. 4: 119. 1957) it would not be justifiable to assume that there is necessarily a direct relationship. Although in the Carolines the Breadfruit is most frequently called *mai*, in the Palau Islands and Yap, which are in the west-



ern part of the group, it is known by the names *medu*, *methu*, *thu*, *su* and other variants which are all probably cognate (Christian, l.c.; Barrau, l.c.). Further east in the group, in Kusaie, it is called *mos* or *mosse*, and this name is also recorded, as *mossi*, for Northeastern New Guinea (Christian, l.c.). No obvious correspondences can be traced in the names of varieties, except between neighbouring islands; thus Niue has evidently received its varieties from Samoa (? or Tonga), while Makatea shows some relationship with Tahiti.

The status and variability of the Breadfruit in the rest of Malaysia, apart from New Guinea and the Moluccas, which have already been discussed, will now be considered. In the Philippines the seeded and seedless forms of the Breadfruit are rather different from each other and they were described by Blanco in 1837 as *A. camansi* and *A. rima* respectively, the specific epithets being derived from their Tagalog vernacular names. (He applied the name *Artocarpus incisus* to the indigenous species now called *A. blancoi*.) The Breadfruit has been regarded as an introduced plant in the islands by some authors, including Merrill (Fl. Manila, 176. 1912, Enum. Philip. Pl. 2: 40. 1923), and this view of its status is supported by the absence of any definite records, either in the literature or on field labels, of its occurrence in the wild, except in secondary vegetation. This may be contrasted with the fairly abundant herbarium material of *A. blancoi* and *A. treculianus*. Merrill's record of *Artocarpus communis* from the Lamao Forest Reserve, Luzon (Philip. Jour. Sci. 1: Suppl. 43. 1906), and Whitford's records of the species as a constituent of dipterocarp forest in various parts of the Philippines (Philip. Jour. Sci. 1: 373-431, 637-679. 1906; l.c. Bot. 4: 699-723. 1909; Bull. Bur. For Philip. 10(1): 23, (2): 29. 1911) must, for the most part, be referred to other indigenous species of this series. However, it appears that the Breadfruit does occur in the degraded forest called *parang* (Whitford, Philip. Jour. Sci. 1: 391. t. 4, 5. 1906).

Quisumbing, however, in 1940 (Philip. Jour. Sci. 72: 331) revived the name *Artocarpus camansi* Blanco for the seeded form of the Breadfruit in the Philippines and expressed the opinion that it was an endemic species, closely related to, but specifically distinct from, the ancestor of the Polynesian Breadfruit. The *camansi* has a narrowly oblong-obovoid male head, 15-25 cm. long, and narrowly conical processes on the syncarp, projecting 5-8 mm., whereas the *rima* (which Quisumbing referred to *A. communis*) has a club-shaped male head (8-15 cm. long in the collections examined in this study) and a nearly smooth syncarp. However, specimens representing the *camansi* which have been examined (e.g., Merrill SB 830) resemble rather closely others seen from New Guinea and, although the seeded breadfruit is apparently naturalized in Luzon, it seems most probable that it has been introduced from New Guinea or the Moluccas. The rather marked differences shown by the seedless *rima* are due to its introduction from a different source, which was almost certainly the Marianas. The seedless *lemai* of Guam resembles the *rima* in the club-shaped male head, the names are cognate, and there was contact with Manila through the Spanish galleons. Wester made this suggestion in 1924 (Philip. Agr. Rev.

17: 24) on the basis of the absence of any mention of the Breadfruit in the Philippines in de Morga's "Sucesos de las Islas Filipinas" (1609) and the inclusion by G. J. Kamel of *Rhymay Marianorum* (together with *Dugdug Marianorum* and *Camangsi*) in his list of Philippine plants (in Ray, Hist. Pl. 3: App. 52. 1704).

The seeded and seedless forms of the Breadfruit are both cultivated in western Malaysia, and they are similar to the forms described by Rumphius in the "Herbarium Amboinense" from the Moluccas and noted above. The seeded form has distinct processes on the syncarp and more or less abundant indumentum, while the seedless form (which may have a few inviable seeds) has an almost smooth syncarp and is glabrous or nearly so. The latter was described by Hasskarl in 1842 as *Artocarpus laevis*. The earliest mention of the Breadfruit in western Malaysia was made in 1642 in a brief description in Bontius' "De Medicina Indorum" (p. 52), which apparently refers to this species, although a remark on the objectionable odour of the fruit suggests some confusion with the Chempedak (*Artocarpus integer*). This description reappeared in Bontius' "Historiae Naturalis & Medicae Indiae Orientalis Libri Sex" (p. 119), as edited and published by Piso in 1658 in his "De Indiae Utriusque Re Naturali et Medica." An illustration of the Breadfruit was added, but the vernacular name was given as *Champidaca*; further reference is made to this confusion under *A. integer*. The three works mentioned in this paragraph, together with Kamel's list, contain the only references in pre-Linnaean botanical writings to the Breadfruit.

The differences just given between the seeded and seedless forms of the Breadfruit seem to hold, with minor variations, throughout the rest of the tropics, but the specimens and descriptions available are not adequate for this to be stated with certainty.

It is not known when the Breadfruit was first carried westward from Malaysia, but it is cultivated in Ceylon and along the western coast of the Deccan peninsula. According to Thunberg (Philos. Trans. Roy. Soc. London 69: 470. 1779) it was introduced into Ceylon in 1727 or 1728 from the Maldive Islands, but no confirmation of this statement has been found in the later literature.

The Breadfruit was introduced to Mauritius from Luzon in the eighteenth century by Sonnerat, who described it under the name *rima* (Voy. Nouv. Guin. 99. t. 57-60. 1776), but it was not established on the African continent until the nineteenth century, according to Chevalier (Revue Bot. Appl. Agr. Trop. 20: 29. 1940). It was mentioned by Ficalho in 1884 (Pl. Uteis Afr. Port. 273) for the Portuguese dependencies and Chevalier (l.c.) states that it was introduced into French Guinea in 1897. It is now common along the coastal region of west tropical Africa.

In the New World, the Breadfruit was introduced into the West Indies at the end of the eighteenth century, following representations by the planters as to its potential value in providing a staple food for the slaves (see Howard, Scientific American 188: 88. 1953). The Society of Arts, in London, offered rewards for its introduction and establishment, and

details of these, with reports on the progress of the trees, appeared in their Transactions for the period 1783–1807. The seeded form was brought to Martinique from Mauritius by a French ship in 1792 (Robley, Trans. Soc. Arts 20: 357. 1802). The introduction of the Breadfruit by Captain William Bligh is, however, far better known. In 1787 he set out from London in the *Bounty*, largely through the influence of Sir Joseph Banks (see Cameron, Sir Joseph Banks, K.B., P.R.S., The Autocrat of the Philosophers. 1952), to collect young plants from Tahiti and carry them westward to the West Indies, but soon after the *Bounty* left Tahiti in 1789 this attempt terminated in the famous mutiny. In 1791 Bligh set out once more in the *Providence* and arrived at St. Vincent and Jamaica in 1793, bringing with him the seedless form of the Breadfruit from Tahiti, together with a few plants of the seeded form from Timor. An illustrated account of both forms, based on material from St. Vincent was published by W. J. Hooker in 1828 (Bot. Mag. 55: t. 2869–71).

In South America, Tavares (Broteria, Ser. Vulg. Sci. 13: 25. 1915) states that the Breadfruit was first cultivated in French Guiana in 1811, and that it was introduced from there to Brazil, where only the seedless form is known. The Breadfruit is also frequently grown in the coastal regions of Central America and, as Standley and Steyermark observe (Fieldiana Bot. 24(4): 12. 1946), it may have been introduced there from the west by early Spanish voyagers.

12. *Artocarpus pinnatisectus* Merr. Philip. Jour. Sci. 18: 50. 1921, "*pinnatisecta*," Enum. Philip. Pl. 2: 43. 1923. Holotype, Luzon, *Escritor* BS 20789 (PNH, destroyed); isotypes (κ, us); lectotype (us).

Tall tree (fide Merrill). *Twigs* 15–20 mm. thick, shallowly rugose, glabrous except for tufts of patent greyish or pale rufous hairs to 3 mm. long below the stipular scars and petioles; stipular scars 2 mm. broad, not prominent, conspicuous; lenticels in a ring below scar. *Stipules* 10–20 cm. long, lanceolate, acute, villous with patent, pale rufous hairs, to 3 mm. long. *Leaves* c. 40–100 × 35–60 cm., oblong to oblong-ovate in outline (fide Merrill), deeply pinnatifid, lateral lobes c. 12–20 pairs, lanceolate, attenuate, to 18 × 2 cm. (*Escritor* BS 20789) or to 38 × 6 cm. (*Ramos & Edano* BS 33536), sinuses narrow, extending to within 1.5 cm. of midrib; midrib and main veins of lateral lobes prominent beneath, reticulum slightly so; glabrous above, main veins appressed-puberulent beneath, and with scattered longer hairs; lateral veins of lobes to c. 25 pairs; intercostals few, parallel or not; drying pale to dark brown; hypodermis absent; gland-hairs immersed, heads flattened, c. 16-celled; petiole 70–100 mm. long.

*Inflorescences* solitary in leaf-axils (only male head seen attached). *Male head* (immature, deformed on both sheets) of two laterally connate lobes each to 70 × 25 mm., smooth, covered with flowers, a few of these sterile, and occasional interfloral bracts, the sterile perianths solid and pro-



jecting c. 0.5 mm. from the surface; perianths tubular, 2.4 mm. long, bilobed, lobes with deflexed inflated hairs having acute tips; stamen immature, filament fairly slender, anther-cells oblong, 1.2 mm. long; bracts slenderly stalked, heads narrowly peltate, 0.2 mm. across, with a tuft of hairs 1 mm. long; peduncle (two laterally fused)  $25 \times 5$  mm., with sparse patent rufous hairs. *Syncarp* (submature)  $15 \times 5$  cm., cylindric, drying red-brown, covered by closely set, fleshy, short-cylindric, obtuse processes,  $3 \times 2$  mm., rough from the acute, deflexed tips of inflated hairs; simple styles exerted to 1.5 mm.; scattered bracts present between the processes, slenderly stalked, heads narrowly peltate, 0.2 mm. across; wall 1.5 mm. thick; seeds . . . ; core 25 mm. across; peduncle . . . .

DISTRIBUTION: Philippine Islands (Luzon and ? Mindanao).

**Philippine Islands.** LUZON. Quezon (Tayabas): Guinayangan, *Escritor BS 20789*, Mar. 1913 (K, US, ♂). Camarines: Paracale, *Ramos & Edano BS 33536* (A, K, US, ♀).

This species is based on very inadequate material. Only two collections have been seen, these bearing immature male inflorescences and a detached, submature syncarp respectively. However, although the specimens differ in the size of their leaves, they agree in the large number of lateral lobes (12–20 pairs as compared with 7–10 pairs in *A. multifidus*), and their association seems justified in view of the differences from the other species already noted under the series. In the original description Merrill cited a third collection, *Cruz FB 27751*, Davao, Mindanao, but no duplicates of this have been found and it was not stated whether it was fertile. Both the isotypes show the same abnormality of the male inflorescence, which has the appearance of two inflorescences fused laterally and presumably developed from a partially divided rudiment. Merrill made no reference to this and gave the dimensions of the head as  $10 \times 3$  cm., and the length of the peduncle as 3 to 4 cm.

13. *Artocarpus multifidus* Jarrett, sp. nov. Holotype, Samar, *Sulit 6462* (PNH); isotype (A).

Inflorescentiae floribus fertilibus, plerisque perianthiis solidis praelongis, bracteisque raris obtectae; folia profunde pinnatifida, laciniis utrinque 7–10, glandulis immersis, capitibus planis 8-cellis, sine hypoderme.

Arbores ad 10 [–20] m. altae. [*Ramuli juniores* 15–20 mm. crassi, rugosi, infra cicatrices stipularum annulatas, 2 mm. latas, prominulas, conspicuas, villosi, pilis patentibus, pallidi-rufis, 3 mm. longis, lenticellisque circum ramulos dispositis. *Stipulae* 18–23 cm. longae, late lanceolatae, acutae, tenuiter villosae, pilis patentibus, pallidi-rufis, 3 mm. longis.] *Folia* [40–] 90 cm. longa, ovati-oblonga, [profunde pinnatifida,] sinusibus angustis, costa tenuiter villosa, in sicco brunnea; laciniae utrinque [7–]10, lanceolatae, leviter falcatae, attenuatae, ad  $32 \times 7$  cm., nervis mediis lateralibusque subtus prominentibus, nervis transversalibus venulisque subtus prominulis, nervis mediis tenuiter villosis, nervis lateralibus utrinque ad



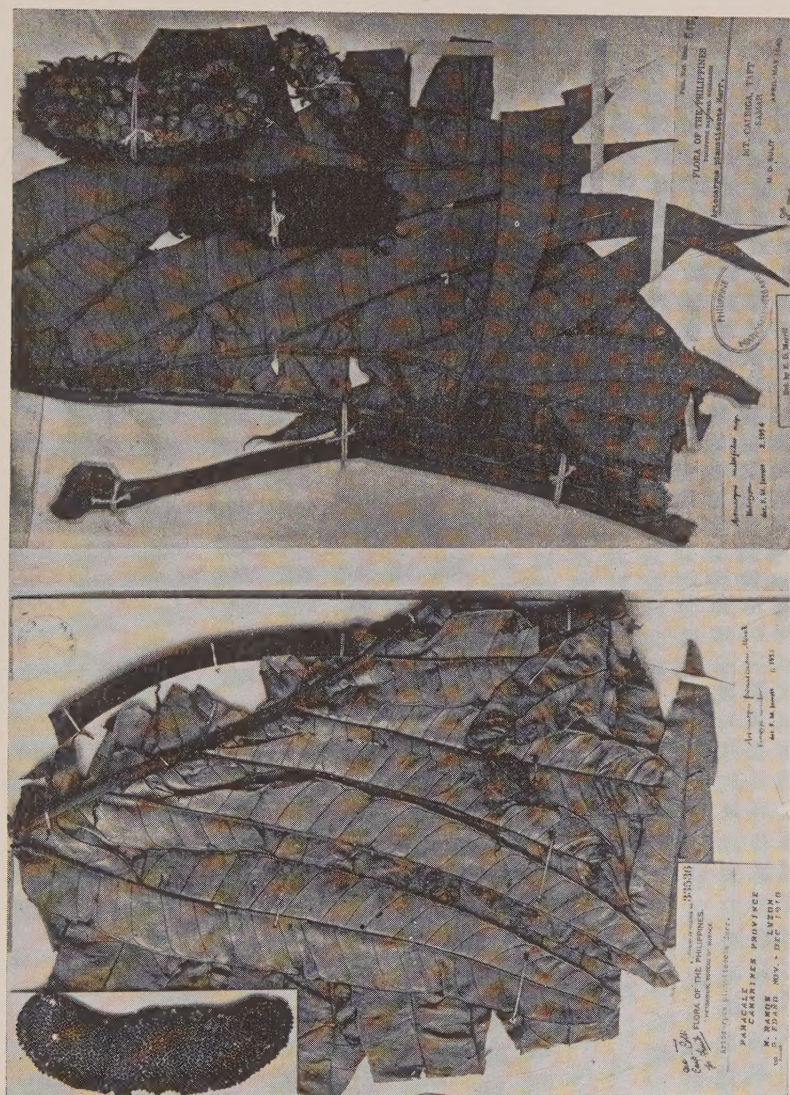


FIG. 13. Left, *Artocarpus pinnatisectus*, paratype, Ramos & Edano 33536 (K); right, *A. multifidus*, holotype, Sulit PNH 6462 (PNH).

25, rectis, pubescentibus, pilis [rectis vel] uncinatis, nervis transversalibus non parallelis; hypodermis absens; glandulae immersae, capitibus planis, 8-cellis; petiolus [70–]130 mm. longus.

*Inflorescentiae* axillis foliorum solitariae. [*Capitula mascula* (immatura) ad  $80 \times 25$  mm., clavata, plana, floribus fertilibus numerosissimis, plerisque sterilibus, 2 mm. exsertis, oblecta; flores fertiles perianthiis tubulosis, 2.5 mm. longis, supra bilobatis, puberulentibus, staminibus filamentis cylindricis, cellis antherum oblongis, 1.5 mm. longis; flores steriles cylindrici, solidi, 4.5 mm. longi (ad 2 mm. prominentes), apicibus clavatis, pilis recurvatis; pedunculus  $50 \times 3$  mm., tenuiter villosus.] *Syncarpium* (maturum)  $12 \times 5$  cm., cylindricum, in sicco brunneum, processibus crebris duarum longitudinum, carnosus, teretibus, obtusis, asperis, pilis recurvatis, subinflatis, inaequalibus, longioribus crispis, oblectum; processus longiores flexuosi,  $15 \times 1$  mm., solidi, breviores  $5 \times 1$  mm., perforati, stylis bifidis, 2 mm. longis exsertis; bractae interflorales rae, tenuissimae, anguste peltatae, capitibus 0.2 mm. latis, pubescentibus; stratum externum syncarpium c. 2 mm. crassum; "semina" (pericarpia indurata) numerosa, ellipsoidea,  $10 \times 7$  mm., stylis sub-basalibus, perianthiis liberis tenuisque inclusa; embryum radícula ventrali, cotyledonibus aequalibus fere in longitudinem positus, testa tenuiter pergamentacea inclusum; axis syncarpium c. 20 mm. diametro; pedunculus  $50 \times 7$  mm., tenuiter villosus.

DISTRIBUTION: in forest to 2000 ft., Philippine Islands (Samar, Mindanao).

**Philippine Islands.** SAMAR. Mt. Calbiga, Taft, *Sulit PNH 6462*, May 1948 (A, PNH, ♀). MINDANAO. Surigao: Mt. Kabatuan, *Mendoza & Convocar PNH 10563* (A, PNH, ♂).

The characters of this rather distinctive species are discussed above, under the series.

(*To be concluded*)